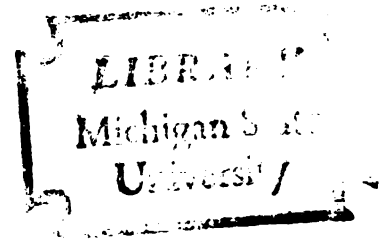


ISLAND-MAINLAND AND WITHIN-SEASON  
COMPARISONS OF COMMUNITY LEVEL  
PARAMETERS AND A MODEL OF  
THEIR INTER-RELATIONSHIPS

Dissertation for the Degree of Ph. D.  
MICHIGAN STATE UNIVERSITY  
JERRY DEXTER HALL  
1974



This is to certify that the  
thesis entitled

Island-Mainland and within Season Comparisons  
of Community Level Parameters  
and a Model of their Inter- Relationships  
presented by

Jerry Dexter Hall

has been accepted towards fulfillment  
of the requirements for

Ph.D. degree in Zoology

Major professor

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## ABSTRACT

### ISLAND-MAINLAND AND WITHIN-SEASON COMPARISONS OF COMMUNITY LEVEL PARAMETERS AND A MODEL OF THEIR INTER-RELATIONSHIPS

By

Jerry Dexter Hall

Differences in five ecological parameters were investigated between island and mainland communities and during the summer season, 1972. These data were also used to test a model of relationships among the parameters that was derived from a review of literature. The parameters, deduced from the structure of food-web diagrams, are (1) Number of Taxa, (2) Evenness of Taxa, (3) Resource Breadth of Animal Taxa, (4) Evenness of Trophic Levels, and (5) Distinctness of Trophic Levels. Data were collected in two pairs of forest floor communities, one pair on North Bass Island in Lake Erie and nearby Marblehead Penninsula, Ohio, and the other pair on South Manitou Island in Lake Michigan and nearby Lelanau Penninsula, Michigan. Organisms studied were herbaceous vascular plants and herbivorous, detritivorous and carnivorous invertebrate animals. Non-parametric analyses of variance of island-mainland differences yielded the following results: Number of Taxa is lower in island communities, possibly due to absence of rare taxa. Resource Breadth may be more influenced by scale of sampling than in insularity or seasonality. Evenness of Trophic Levels is higher in mainland communities than in island communities. Distinctness of Trophic Levels is higher in mainland communities in Ohio, but lower in Michigan, and increases during the summer season. To test the model of relationships among the parameters, ten predictions were made of correlation among them. Predictions were

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tested by partial correlation analyses applied to the data. Six predictions were not refuted and were partially or completely verified. Four were refuted, two with little confidence. A third refuted prediction appears to clarify, rather than refute, the relationship predicted. The structure of the model and existence of the relationships are accepted, and the model is revised and awaits further test. These community-level relationships modeled and tested are complex and consistent and require investigation of mechanisms.

1

ISLAND-MAINLAND AND WITHIN-SEASON COMPARISONS  
OF COMMUNITY LEVEL PARAMETERS  
AND A MODEL OF THEIR INTER-RELATIONSHIPS

By

Jerry Dexter Hall

A DISSERTATION

Submitted to  
Michigan State University  
in partial fulfillment of the requirements  
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1974

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## ACKNOWLEDGMENTS

I wish to express sincere appreciation to Drs. Rollin Baker, John King, Walter Conley, Peter Murphy and William Cooper for the inspiration they have provided throughout my graduate career and for the advice they have rendered during this study. In addition, Dr. Rollin Baker obtained funds for the field work and Dr. William Cooper provided funds for use of the Michigan State University Computer Laboratory.

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The Michigan State University Museum provided some field equipment and facilities, while the Ohio State University Instruction and Research Computer Center provided computing facilities and services. The Society of Sigma Xi, Michigan State University Chapter, granted funds used to obtain identification of animal specimens.

I would like to acknowledge and thank Terry Truax, who provided valuable statistical and computer programming advice; David Dennis, whose artistic skill provided most of the figures, and many friends and various students, who volunteered their help in various parts of the field work, identification and handling of specimens and drawing of figures.

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provided permission  
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advice, and the  
Bass Community;  
Stocking Land Co  
transportation

Lastly and  
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her tolerance



I would also like to acknowledge and thank Joseph Mahler, who provided permission to work in the woodlot studied as the Marblehead Community; Mr. and Mrs. Paul Stonerook, who provided encouragement, advice, and the permission to work in the woodlot studied as the North Bass Community; Graham Downer and the Sleeping Bear Dune Park of the Stocking Land Company, and John Brown, who furnished advice and transportation in the area studied as the South Manitou Community.

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## INTRODUCTION

In this study, food-web ecology was investigated in forest floor communities on islands and mainlands of Lake Erie and Lake Michigan during the summer season of 1972. A portion of each community was studied as a sub-set of the whole community. This portion, or sub-web, included the herbaceous green plants and selected invertebrate animals associated with them. The investigation focused on five ecological parameters that can be deduced from the structure of a food-web diagram. These five parameters are (1) the number of taxa composing a given food web, (2) the evenness of the abundances of those taxa, (3) the average breadth of resources used by consumer taxa, (4) the evenness of the distribution of the taxa among trophic levels, and (5) the distinctness with which the various trophic levels are determined. These parameters are herein labeled respectively with the following terms: (1) Number of Taxa, (2) Evenness of Taxa, (3) Resource Breadth, (4) Evenness of Trophic Levels, and (5) Distinctness of Trophic Levels. It is recognized that these parameters are sufficiently general that each can be approached in a variety of ways. For purposes of this study, each of these parameters was estimated quantitatively by two or more kinds of measurements in each community. These measurements, designed to estimate the parameters, are herein called variables to distinguish them from the parameters they estimate. The parameters and the variables are described in more detail in later sections of this report.

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This study has two goals; one is primarily descriptive, the other experimental. The first goal is to examine the five parameters listed above for any pattern of differences between mainland and island and during the summer season. Numerous authors deal with such insular and seasonal patterns of differences, especially with respect to Number of Taxa and Resource Breadth, and predictions can be made of expected differences. These expected differences are explored in a later section.

The second goal of this study is to develop from the literature and test experimentally a model of relationships among the five ecological parameters presented in the opening paragraph. Predictions of relationships between pairs of these parameters are developed from the model and tested by partial correlation analyses. Additionally, the question is asked whether relationships indicated by these correlation analyses can be explained by influences of insularity or seasonality. Studies by previous authors have dealt with one or perhaps several of the five parameters considered here, but investigations of interactions among them, at the level of community function, are few. Examples of such studies are those by Paine (1966), who has shown that a top level predator can influence the number of species in lower trophic levels, at least in certain intertidal invertebrate communities, and by Wiegert and Owen (1971), who suggest a modified trophic model to explain differences in density levels and in regulatory mechanisms of species of different trophic levels. Other studies of interactions among community parameters, dealing with various parameters, are those by Leigh (1965) and MacArthur (1970), who have mathematically treated the relationships among diversity, productivity, stability, and other parameters, and by Connell and Orias

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## COMMUNITIES STUDIED

### Communities

Communities studied include two mainland-island pairs of forest floor communities. One pair of these communities is located in northern Ohio; the other is located in west-central Michigan (Fig. 1).

The Marblehead Community is the mainland community of the Ohio replicate. It is located on Marblehead Peninsula, Ottawa County, Ohio, approximately one and one-quarter kilometers north of the Sandusky Bay Bridge (U.S. 2), and six and two-thirds kilometers east of Port Clinton, Ohio (Fig. 2). This community is an irregularly shaped wood-lot approximately 9.3 hectares (23 acres) in area and is surrounded by cultivated fields (see Figure 3). The topography is regular, and two small areas are somewhat marshy, possibly indicating a water table near the surface. The canopy layer of the woodlot is dominated by pin oak (Quercus palustris), sugar maple (Acer saccharum), white oak (Quercus alba), and hackberry (Celtis occidentalis). At the time of the study, the ground cover was frequently dense and dominated by poison ivy (Rhus toxicodendron). The woodlot had not been lumbered or grazed for approximately 35 years (Mahler, 1972).

The North Bass Community is the island community of the Ohio replicate. North Bass Island, assigned to Ottawa County, is located (Fig. 2) in Lake Erie about ten and two-thirds kilometers north of the Catawba-Marblehead peninsula and has an approximately two kilometers average diameter (Fig. 2). It is third in a series of three islands extending north from the mainland. The North Bass Community is a woodlot about 13.5 hectares (33.3 acres) in area which extends inland from the western shore of the island and is bordered on three sides by cultivated

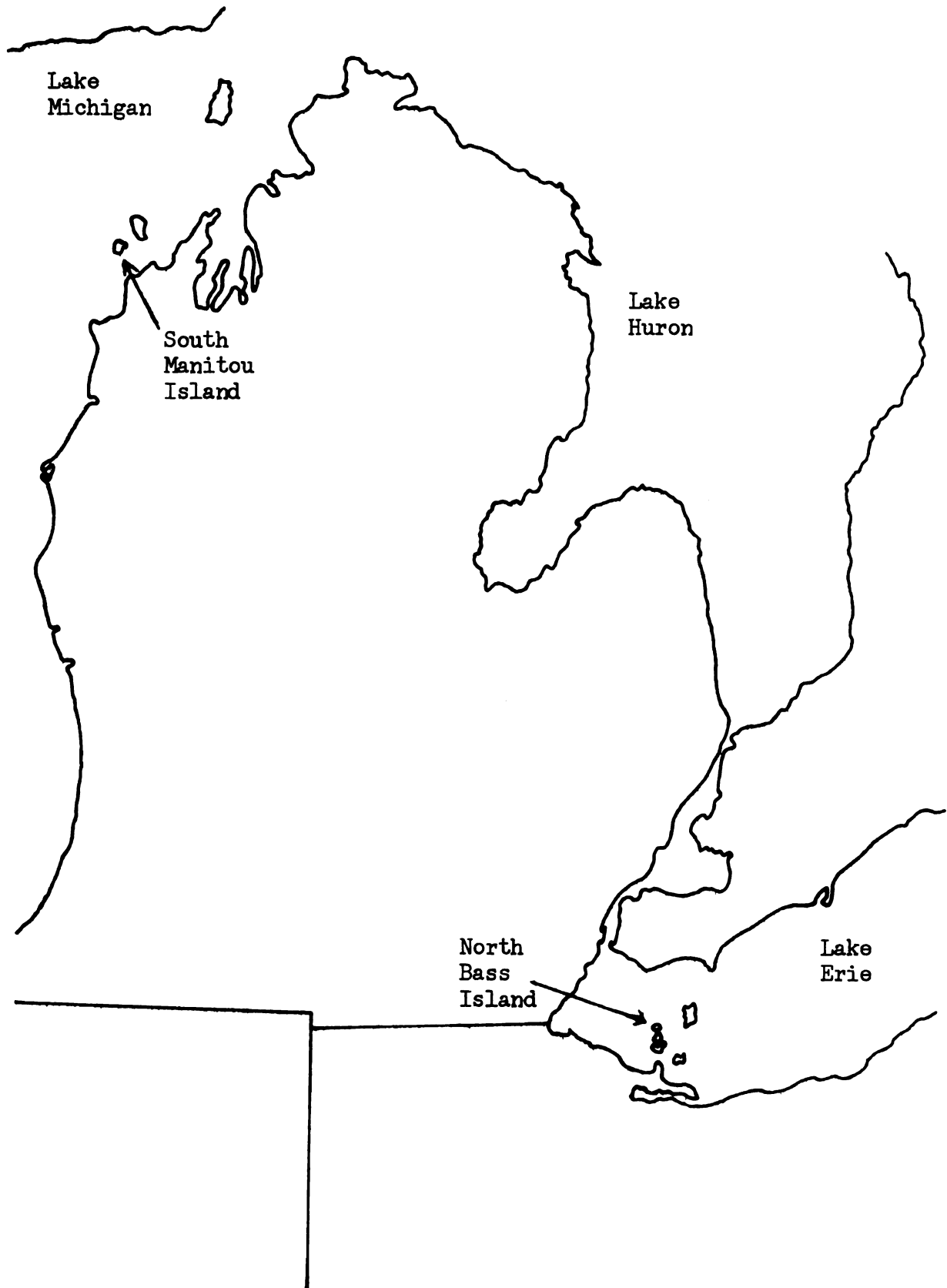


Figure 1. Map of Great Lakes Region Showing All Communities Studied.

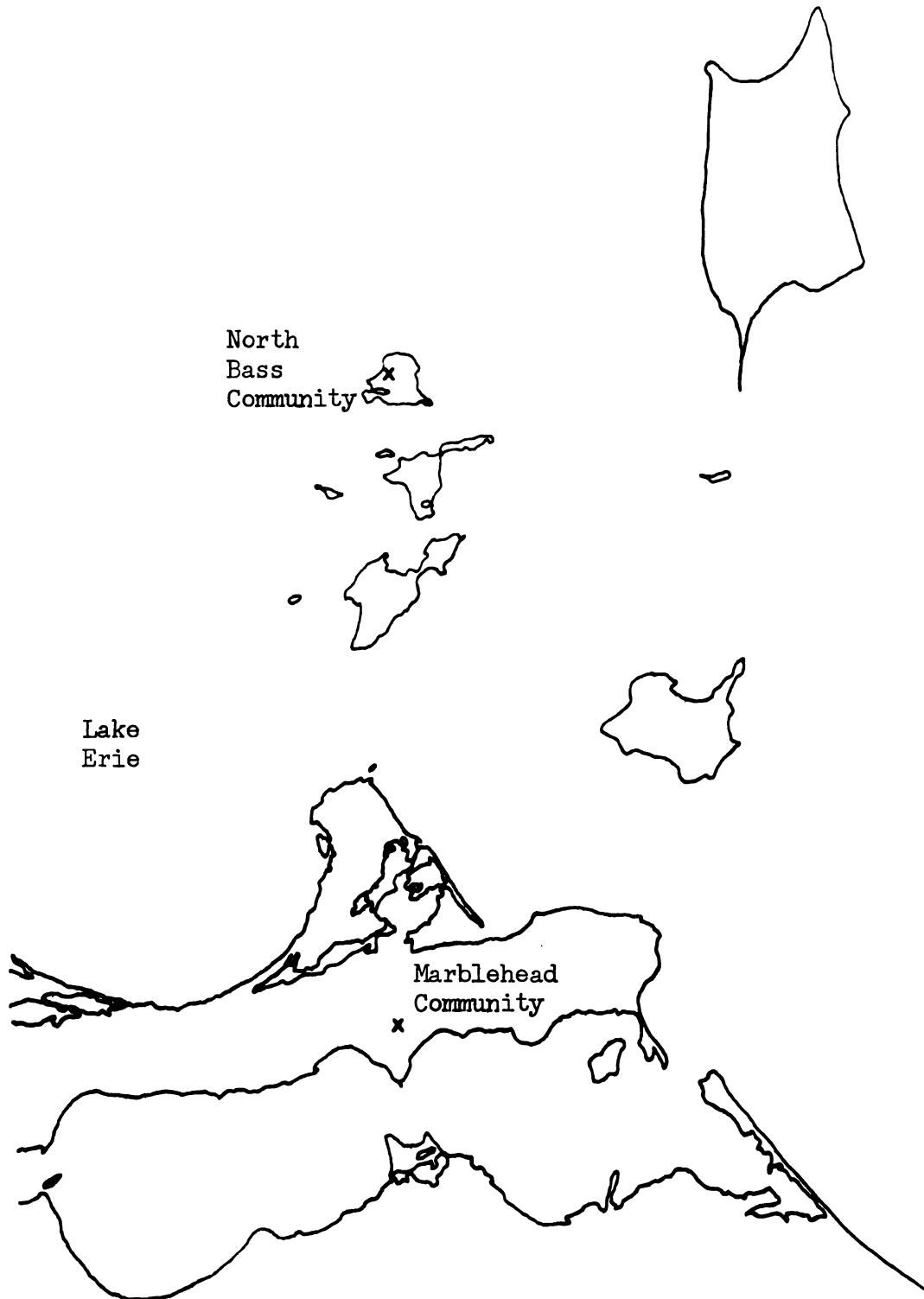


Figure 2. Western Lake Erie Showing the Two Ohio Communities.

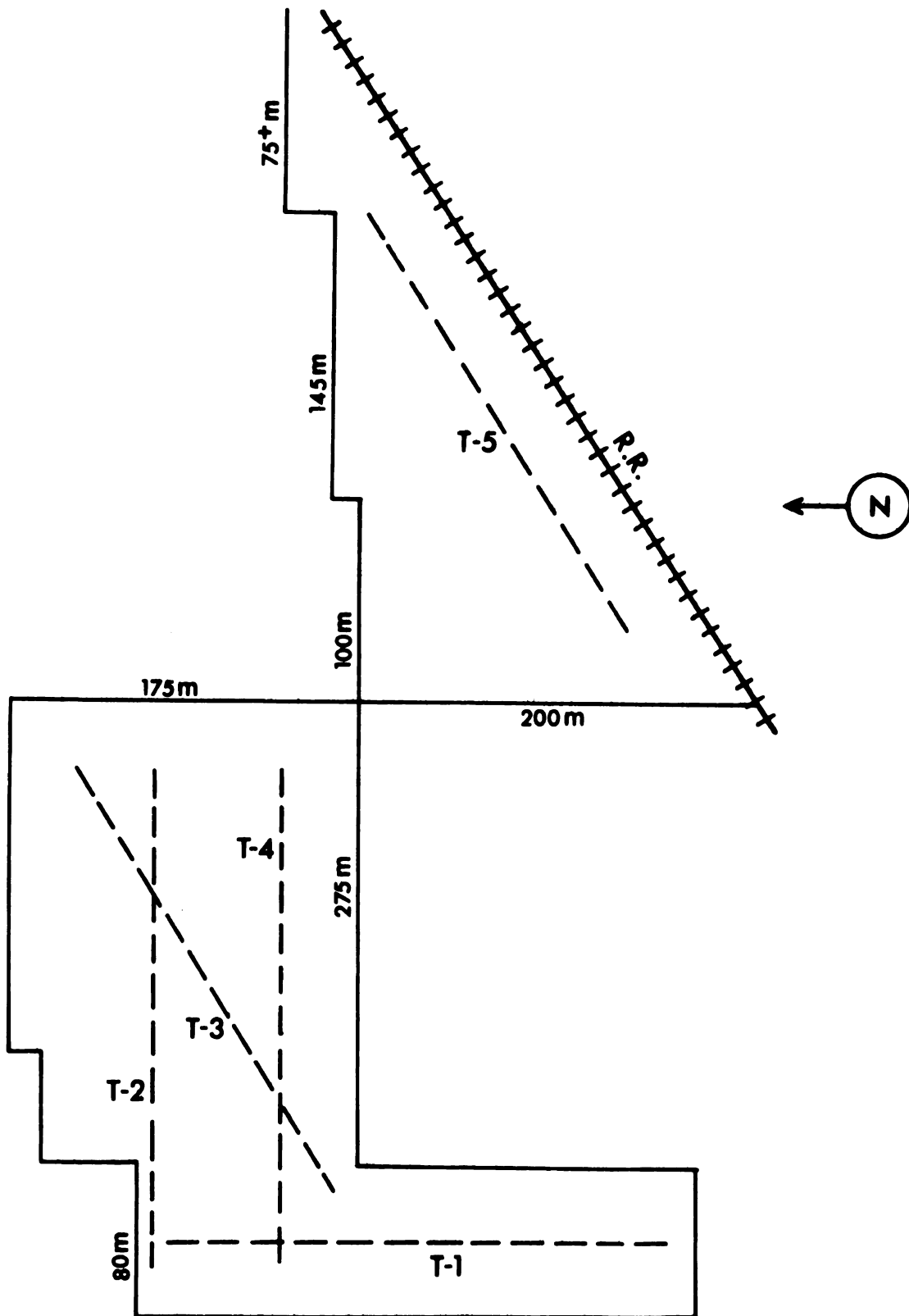


Figure 3. Marblehead Community and Pattern of Transects.



land or mowed grass air-strip (see Figure 4). The topography is as regular as that of the Marblehead Community. However, the water table appears to be lower, despite the closer proximity to the lake. Also, the substrate appears more rocky than in the Marblehead Community. The canopy layer is dominated by American basswood (Tilia americana), sugar maple (Acer saccharum), and hackberry (Celtis occidentalis). At the time of the study, the ground cover was frequently sparse, and was not clearly dominated by any specific species of plants. This wood-lot had not been lumbered or grazed for approximately fifty years (Stonerook, 1972).

The Leelanau Community is the mainland community of the Michigan replicate. This community is located in the southwestern portion of Leelanau Peninsula, Leelanau County, Michigan (Fig. 5). It is approximately five kilometers north of Empire, Michigan, one and one-third kilometers southwest of Glen Lake, and one and one-fourth kilometers east of Lake Michigan. The site studied is part of a forest system that extends north and south for several kilometers, and is about two-thirds kilometer inland from an active front of Sleeping Bear Dune. The topography consists of a series of low parallel ridges running approximately north-west to south-east. The soil is sandy beneath the organic laden top layer. The forest canopy is dominated primarily by sugar maple (Acer saccharum) and beech (Fagus grandifolia). At the time of the study, the ground cover was consistently dense and was quite diverse, although dominated in some areas by maple seedlings. The site of the study has not been lumbered or grazed for over twenty-five years (Downer, 1972).

The South Manitou Community is the island community of the Michigan replicate of the study. South Manitou Island, assigned to Leelanau

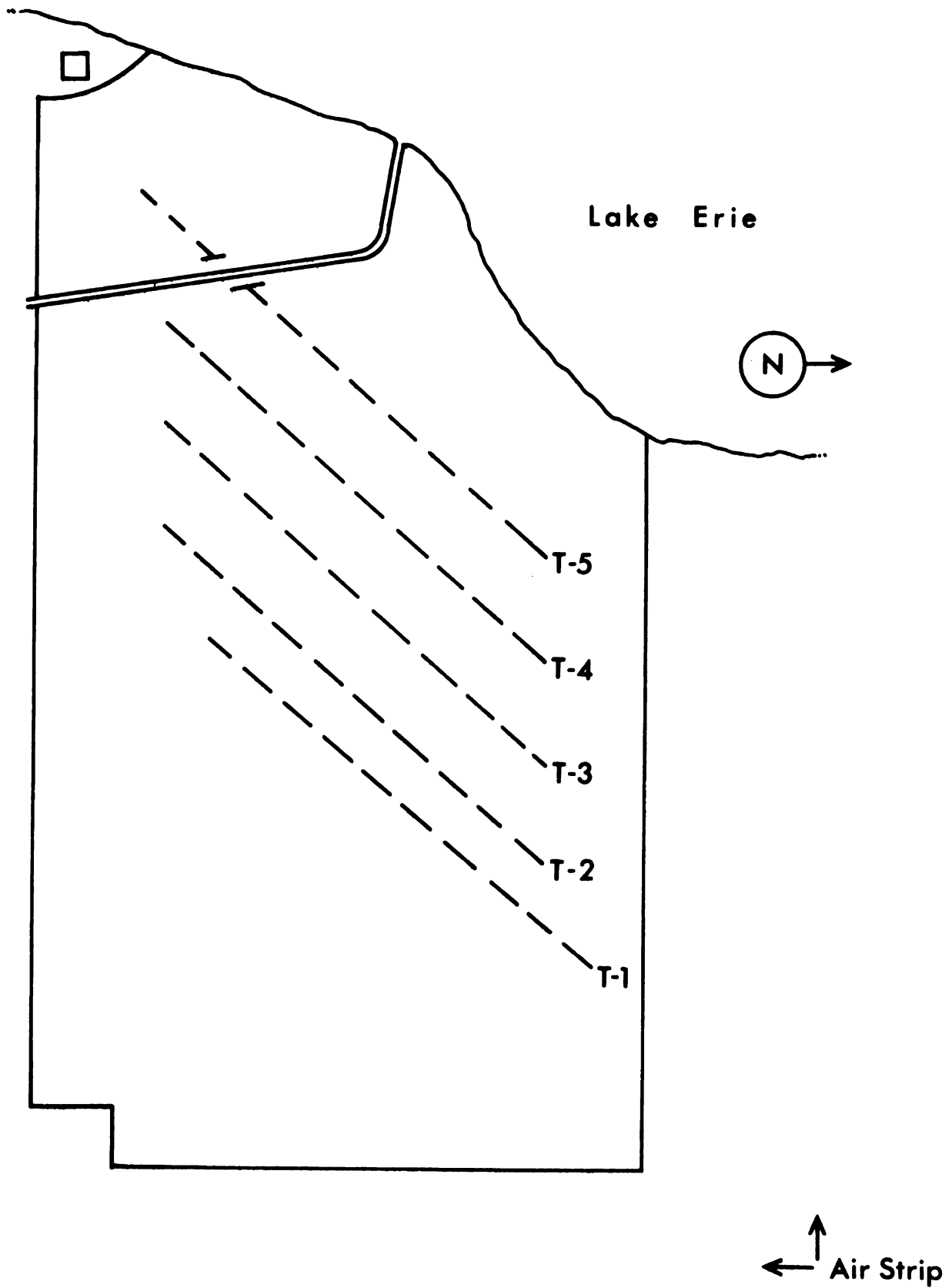


Figure 4. North Bass Community and Pattern of Transects.

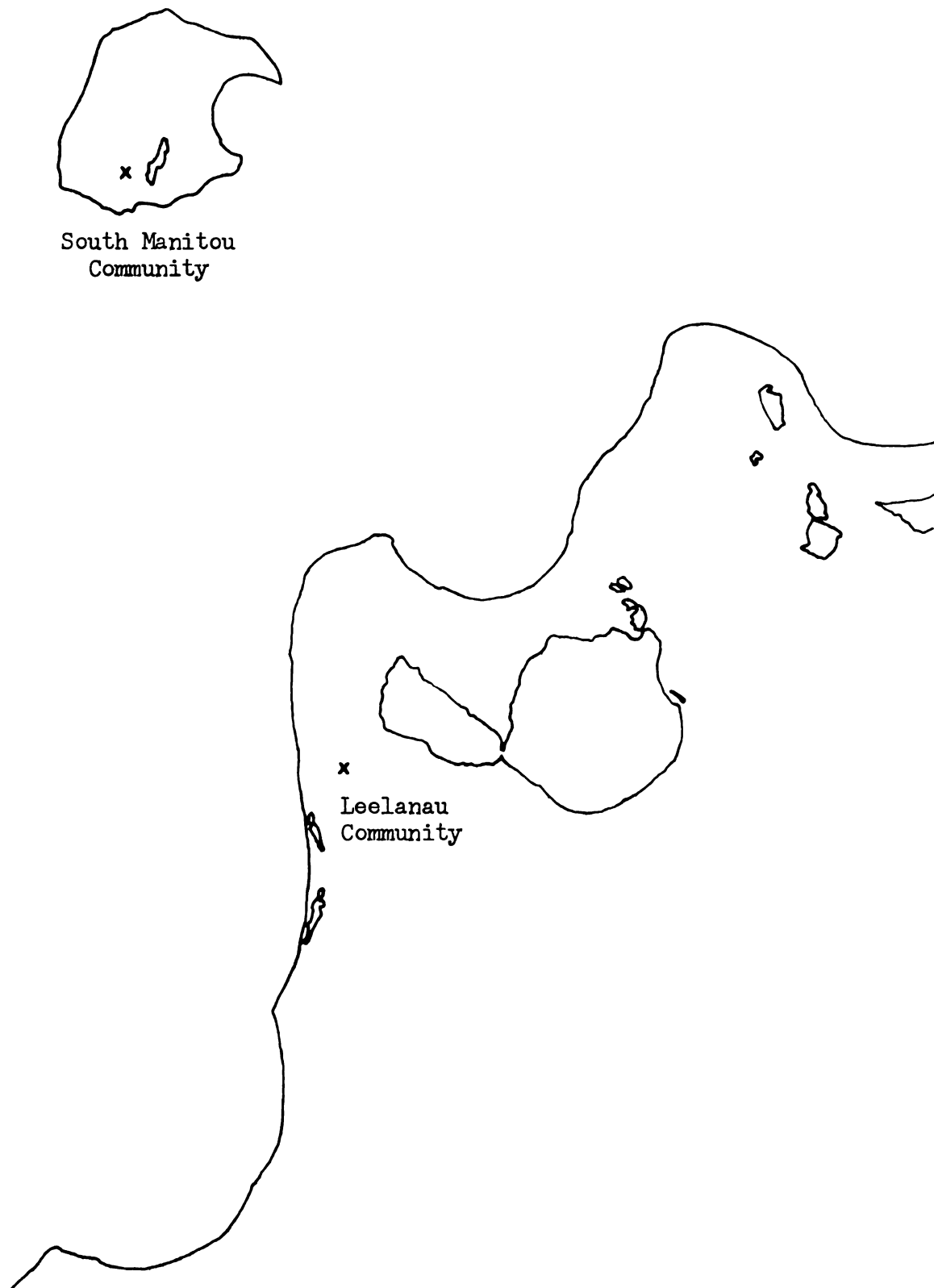


Figure 5. Northern Lake Michigan Showing the Two Michigan Communities.

County, is located in Lake Michigan approximately ten and a half kilometers west of Leelanau Peninsula, slightly north of the Leelanau Community study site (Fig. 5). The study site on South Manitou is about two-thirds kilometers west of the southern end of Lake Florence, one and two-thirds kilometers east of the island's western shore and about two-thirds kilometer north of its southern shore. The site is about one and one-third kilometers east of the high stable dunes forming the western shore of the island. The topography consists of parallel ridges, as on Leelanau Peninsula, but with slightly more exaggerated relief and with a slight general slope south-eastward, parallel with the ridges. The soil, as on Leelanau Peninsula is sandy beneath the organic top layer. The forest canopy is dominated by sugar maple (Acer saccharum), beech (Fagus grandifolia), and some yellow birch (Betula lutea). At the time of the study the ground cover, as on Leelanau Peninsula, was consistently dense and diverse. This portion had not been logged for approximately forty-five years (Brown, 1972).

### Transects

In each of the communities studied, five belt transects were established. Each transect was 250 meters long and one-half meter wide. Where possible, these transects were established in a pattern parallel to one another.

In the Marblehead Community, the five transects were laid out along four different directions to best fit the woodlot (Fig. 3). Transects were placed so that all parts of all transects were at least fifteen meters into the woodlot from its edge. In this community only, some transects intersected.

In the North Bass Community, the five transects were established parallel to one another and to the western lake shore (Fig. 4). The transects were separated from one another by fifty meters or more and were at least 150 meters from the lake-shore.

In the Leelanau Community, the five transects were established parallel to the active dune front and parallel to each other, and were perpendicular to the low parallel ridges (Fig. 6). The transects were separated by fifty meters or more. Two transects extended near a paved road where the tree canopy had been cut.

In the South Manitou Community the transects were established parallel to the dunes which form the western shore of the island (Fig. 7). This pattern also placed them perpendicular to the parallel ridges and to the slight elevation gradient. From a central east-west axis, two transects extended northward in a parallel fashion while three transects extended southward in a parallel fashion. Parallel transects were seventy-five meters apart, and the near ends of transects either side of the central axis were separated in a north-south direction by 100 meters.

For purposes of data collection, each transect was divided into twenty-five sections, ten meters each, called plots. Fifteen of these plots constituted the basic units of data collection for each transect. Each of these plots was further sub-divided into ten one-meter sub-plots. Of these ten sub-plots, five were randomly chosen in each plot for collection of plant data.

#### Organisms Studied

Organisms investigated in this study include the vascular green plants

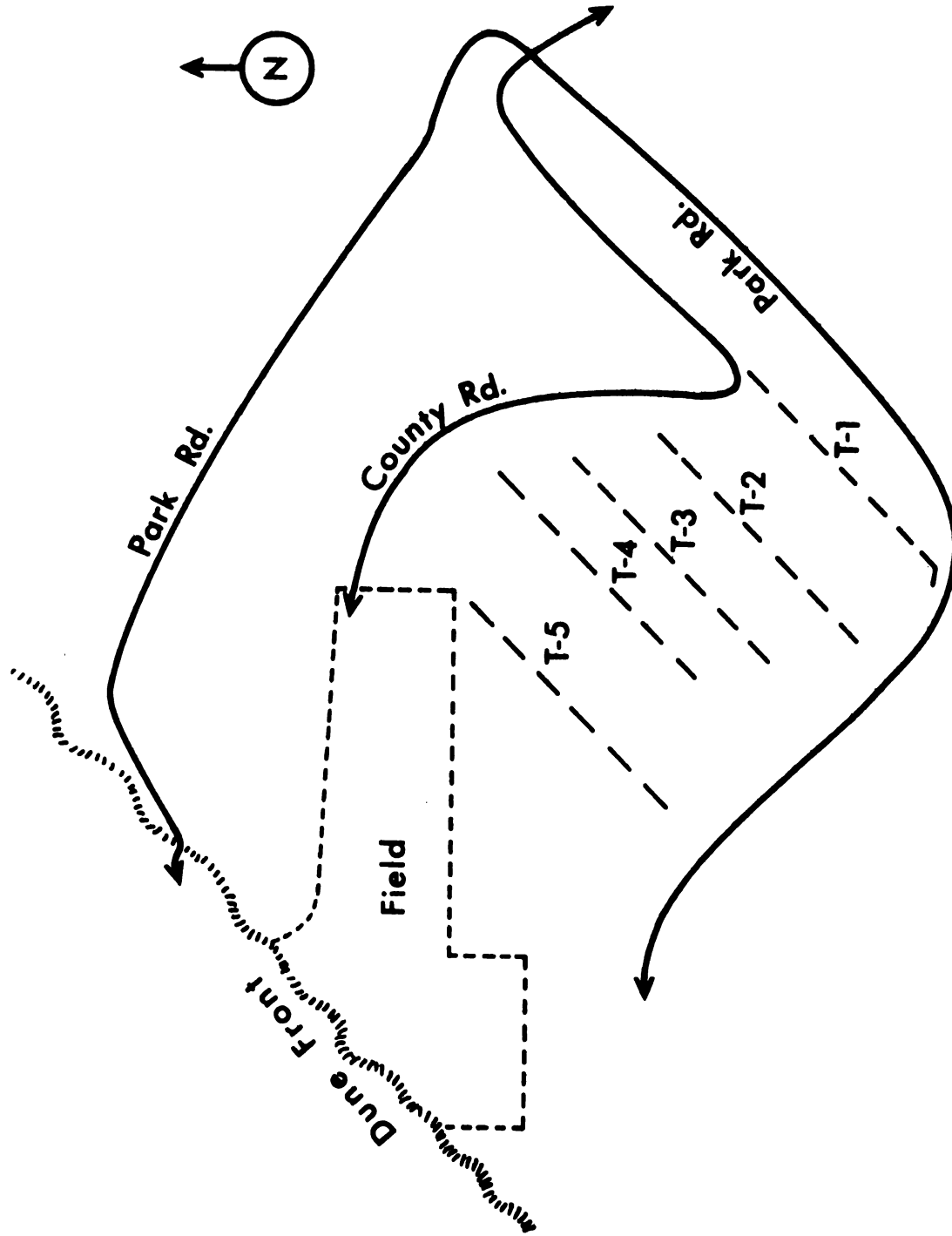


Figure 6. Leelanau Community and Pattern of Transects.

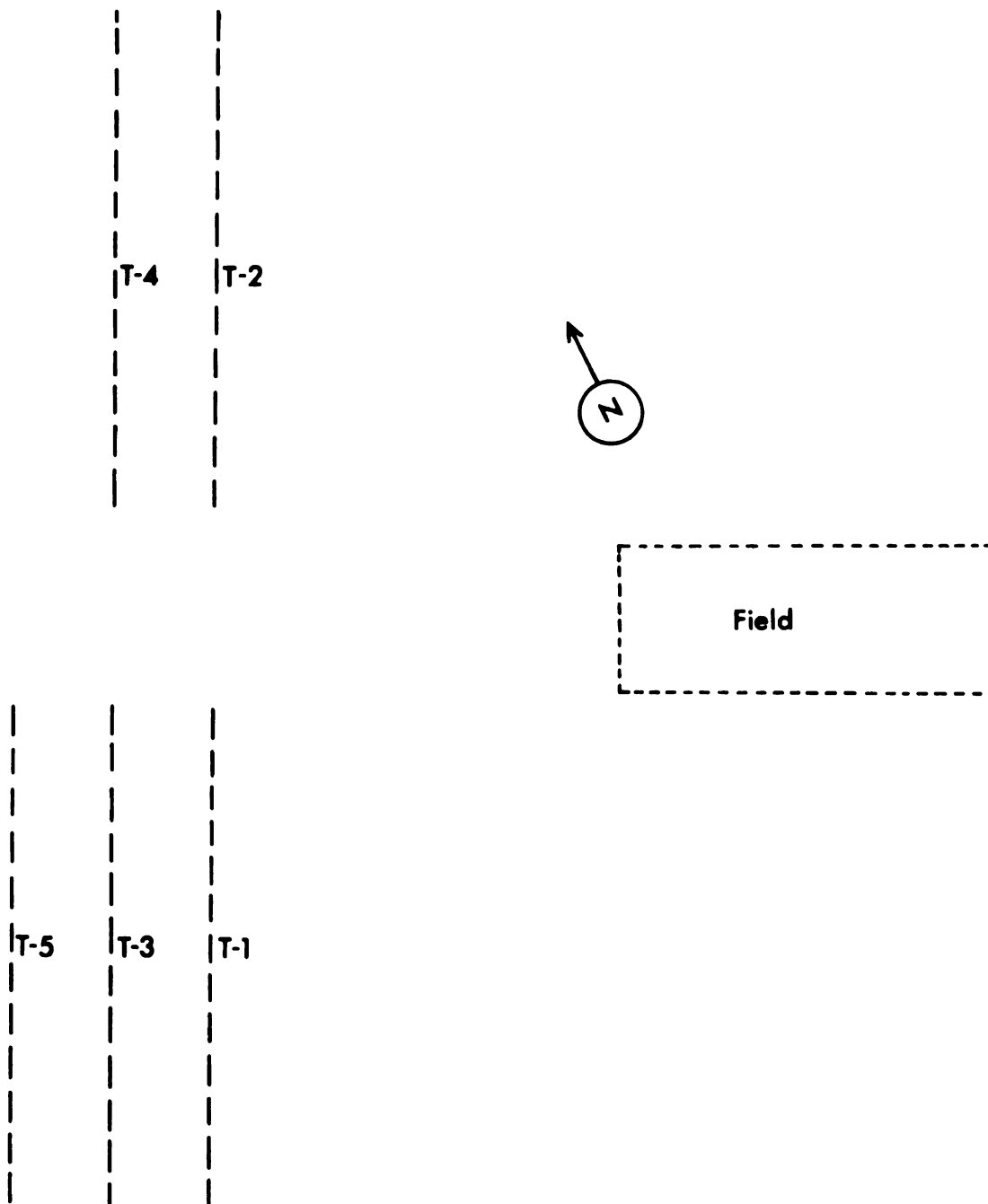


Figure 7. South Manitou Community and Pattern of Transects.

of the herbaceous layer of vegetation, and invertebrate animals collected in association with this layer.

Plants with a one and one-quarter centimeter or less basal diameter were defined for the sake of study as herbaceous plants. Plant data were collected in the form of frequency data. The frequency of sub-plots per plot in which a given species occurred was recorded for all plant species present. Actual numbers of individual plants per plot were not used as data because of the difficulty of defining an individual in some plants, such as vines and cluster-forming plants. The sub-plot dimensions were selected on the basis of a pilot experiment in which the number of species was determined cumulatively in nested quadrats of increasing size, from twelve centimeters by six centimeters to four meters by two meters. The quadrat size at which the variance in cumulative species number, among five sets of nested quadrats, stopped increasing was one meter by one-half meter. These dimensions were those used for the sub-plot sizes in this study. Table 1 is a list by community of plant species found.

Invertebrate animals investigated in this study were those collected in pit-fall traps placed on the forest floor beneath the herbaceous vegetation. One pitfall trap was placed along each plot of each transect, approximately near the center of the plot. These traps were ten centimeter deep waxed cardboard cups with a ten centimeter bottom diameter. They were placed such that the top edge of each trap was flush with the level of the surrounding soil, and they were filled to a depth of one and one-half centimeter with industrial grade ethylene glycol as a killing agent and a temporary preservative. Traps were left operative in the forest floor for seventy-two hours. Specimens were later transferred to seventy percent ethanol and then identified to family (in the cases of



Table 1. List of Plant Species and Their Occurrences by Community and Visit.

SPECIES	COMMON NAME	M	NB	L	SM
<u>Rhus toxicodendron</u>	poison ivy	X	X	0	0
<u>Rhus typhina</u>	staghorn sumac	X	X	0	0
<u>Galium aparinus</u>	cleavers	X	X	0	0
<u>Galium boreale</u>	northern bedstraw	X	0	0	0
<u>Galium triflorum</u>	fragrant bedstraw	0	0	X	X
<u>Galium lanceolatum</u>	yellow wild licorice	0	0	X	0
<u>Mitchella repens</u>	partridge berry	X	X	0	0
<u>Lonicera villosa</u>	fly honeysuckle	X	0	0	0
<u>Lonicera canadense</u>	Canada honeysuckle	0	0	X	X
<u>Cornus alternifolia</u>	alternate leaf dogwood	X	0	X	0
<u>Cornus drummondii</u>	rough-leaf dogwood	0	X	0	0
<u>Cornus sp.</u>	dogwood	X	0	0	0
<u>Ulmus rubra</u>	slippery elm	X	X	0	0
<u>Ostrya virginiana</u>	ironwood	0	0	X	X
<u>Crataegus spp.</u>	Hawthorne	X	0	0	0
<u>Celtis occidentalis</u>	hackberry	X	X	0	0
<u>Pyrus coronaria</u>	pear	0	X	X	X
<u>Prunus serotina</u>	black cherry	0	X	0	0
<u>Prunus virginiana</u>	choke cherry	0	X	X	X
<u>Rubus occidentalis</u>	black raspberry	0	X	0	0
<u>Rubus strigosus</u>	red raspberry	0	0	X	0
<u>Rubus sp.</u>	black berry	X	0	0	0
<u>Rosa setigera</u>	prairie rose	X	0	0	X
<u>Rosa palustris</u>	swamp rose	X	0	0	X
<u>Rosa carolina</u>	pasture rose	X	0	0	0

Table 1. Continued.

SPECIES	COMMON NAME	M	NB	L	SM
<u>Rosa sp.</u>	rose	0	X	0	0
<u>Duchesnea indica</u>	Indian strawberry	X	0	0	0
<u>Potentilla simplex</u>	cinquefoil	X	0	0	0
<u>Fragaria virginiana canadensis</u>	common strawberry	0	0	X	0
<u>Geum canadense</u>	white avens	X	X	0	0
<u>Sanicula canadensis</u>	black snake root	X	X	X	0
<u>Ribes americanum</u>	black current	X	0	0	0
<u>Ribes cynosbati</u>	pasture goosberry	0	0	X	X
<u>Juglans nigra</u>	black walnut	X	0	0	0
<u>Carya cordiformis</u>	bitternut hickory	X	0	0	0
<u>Carya ovalis</u>	pignut hickory	X	0	0	0
<u>Carya ovata</u>	shag-bark	0	X	0	0
<u>Fagus grandifolia</u>	beech	0	0	X	X
<u>Quercus alba</u>	white oak	X	0	0	0
<u>Quercus palustris</u>	pin oak	X	0	0	0
<u>Quercus velutina</u>	black oak	0	0	X	0
<u>Fraxinus pennsylvanicus subintegerrima</u>	green ash	X	X	X	X
<u>Xanthophyllum americanum</u>	northern prickly ash	X	0	0	0
<u>Acer saccharum</u>	sugar maple	0	X	X	X
<u>Acer nigrum</u>	black maple	0	X	X	0
<u>Acer spicatum</u>	mountain maple	0	0	0	X
<u>Betula lutea</u>	yellow birch	0	0	X	X
<u>Betula papyrifera</u>	white birch	0	0	X	0
<u>Carpinus caroliniana</u>	blue beech, ironwood	X	X	0	0

Table 1. Continued.

SPECIES	COMMON NAME	M	NB	L	SM
<u>Tilia americana</u>	American basswood	X	X	X	O
<u>Sambucus canadensis</u>	common elder	X	X	X	X
<u>Viburnum acerifolium</u>	maple-leaf viburnum	O	O	X	X
<u>Ailanthus altissima</u>	tree of heaven	O	X	O	O
<u>Vitis palmata</u>	cat grape	X	X	X	O
<u>Campsis radicans</u>	trumpet creeper	X	X	O	O
<u>Menispermum canadense</u>	canada moonseed	X	O	O	O
<u>Solanum dulcamara</u>	bitter nightshade	O	X	O	O
<u>Parthenocissus quinquefolia</u>	Virginia creeper	X	X	O	O
<u>Solidago sp.</u>	goldenrod	X	X	X	X
<u>Hydrophyllum virginianum</u>	virginia waterleaf	X	X	X	X
<u>Arisaema triphyllum</u>	jack-in-the-pulpit	X	O	X	X
<u>Arisaema dracontium</u>	green dragon	X	O	O	O
<u>Smilax ecirrhata</u>	carrion flower	X	X	O	O
<u>Lysimachia ciliata</u>	fringed loosestrife	X	O	O	O
<u>Boehmeria cylindrica</u>	bog-hemp	X	O	O	O
<u>Leonurus cardiaca</u>	motherwort	O	X	O	O
<u>Arctium minus</u>	common burdock	O	X	X	X
<u>Gratiola aurea</u>	hedge hyssop	X	X	O	O
<u>Osmorhiza longistylis</u>	sweet cicily	O	X	X	X
<u>Geranium robertianum</u>	Herb Robert	X	X	O	X
<u>Mitella diphylla</u>	mitrewort	X	X	X	X
<u>Arabis perstellata</u> va. <u>shortti</u>	rock cress	O	X	O	O
<u>Campanula americana</u>	tall bellflower	O	X	O	O
<u>Aralia nudicaulis</u>	sarsaparilla	O	O	X	X

Table 1. Continued.

SPECIES	COMMON NAME	M	NB	L	SM
<u>Caulophyllum thalictroides</u>	blue cohosh	0	0	X	X
<u>Thalictrum dioicum</u>	early meadow-rue	0	0	X	X
<u>Actaea alba</u>	white baneberry	0	0	X	X
<u>Polygonum virginianum</u>	Virginia knotweed	X	0	0	0
<u>Impatiens biflora</u>	jewel weed	X	0	0	0
<u>Impatiens sp.</u>	touch-me-not	X	0	0	0
<u>Phryma leptostachya</u>	lopseed	X	X	0	0
<u>Chenopodium album</u>	lamb's quarters	0	X	0	0
<u>Solanum nigrum</u>	black nightshade	0	X	0	0
<u>Heracleum lanatum</u>	cow parsnip	0	0	0	X
<u>Viola canadensis</u>	Canada violet	X	X	X	X
<u>Viola pubescens</u>	downy yellow violet	X	X	X	X
<u>Viola renifolia</u>	kidney-leaved violet	X	0	0	0
<u>Viola incognita</u>	large-leaved violet	X	X	0	0
<u>Viola eriocarpa</u>	smooth yellow violet	X	X	X	X
<u>Viola conspersa</u>	American dog-violet	0	0	X	X
<u>Viola selkirkii</u>	great-spurred violet	0	0	0	X
<u>Viola sp.</u>	violet	0	0	0	X
<u>Viola papilionacea</u>	common blue violet	X	X	0	0
<u>Coptis trifolia</u>	gold thread	X	X	0	0
<u>Oxalis sp.</u>	sorrel	X	X	0	0
<u>Dentaria dyphylla</u>	toothwort	0	0	X	X
<u>Sanguinaria canadensis</u>	bloodroot	0	0	X	X
<u>Hepatica acutiloba</u>	sharp lobed hepatica	0	0	X	X
<u>Pyrola sp.</u>	shinleaf	0	0	X	0

Table 1. Continued.

SPECIES	COMMON NAME	M	NB	L	SM
<u>Habenaria orbiculata</u>	round-leaved orchid	0	0	X	0
<u>Epipactus latifolia</u>	helleborrine	0	0	X	0
<u>Trillium grandiflorum</u>	white trillium	X	0	X	X
<u>Trillium erectum</u>	purple trillium	0	0	X	0
<u>Maianthemum canadense</u>	Canada mayflower	X	0	X	X
<u>Polygonatum pubescens</u>	Solomon's seal	0	0	0	X
<u>Polygonatum caniliculatum</u>	Great Solomon's Seal	0	0	X	0
<u>Polygonatum biflorum</u>	Solomon's-seal	0	0	X	X
<u>Polygonatum multiflorum</u>	Great Solomon's-seal	0	0	X	X
<u>Smilacina racemosa</u>	False Solomon's seal	0	0	X	X
<u>Streptopus roseus</u>	rose twisted-stalk	0	0	X	X
<u>Uvularia grandiflora</u>	large-flowered bellwort	0	0	X	0
<u>Allium tricoccum</u>	wild leek	0	X	X	X
<u>Allium canadense</u>	wild onion	0	X	0	0
<u>Typha sp.</u>	cattail	X	0	0	0
<u>Carex plantaginea</u>	broad-leaved sedge	0	0	X	X
<u>Carex sp.</u>	sedge	X	X	0	0
<u>Carex convolute</u>	sedge	X	X	X	X
<u>Carex sp.</u>	sedge	0	0	X	X
<u>Carex sp.</u>	sedge	X	0	0	0
<u>Carex sp.</u>	sedge	X	0	0	0
<u>Juncus sp.</u>	rush	X	0	0	0
<u>Leersia oryzoides</u>	rice cut grass	X	X	0	0
<u>Oryzopsis vacemosa</u>	rice grass	0	0	0	X
<u>Elymus virginicus</u>	virginal wild rye	0	X	0	0

Table 1. Continued.

SPECIES	COMMON NAME	M	NB	L	SM
<u>Milium effusum</u>	grass	0	0	X	0
<u>Cinna arundinacea</u>	grass	X	0	0	0
<u>Taxus canadensis</u>	American yew	0	0	0	X
<u>Dryopteris sp.</u>	Austriaca* sword fern	0	0	X	X
<u>Adiantum pedatum</u>	maiden hair fern	0	0	X	X
<u>Botrychium virginiana</u>	rattlesnake fern	0	0	X	X
plus distinct but unidentified species		X	X	X	X

Columns M, NB, L, and SM indicate the communities: Ohio mainland, Ohio island, Michigan mainland, Michigan island, respectively. Under these columns is placed an X if the taxon was encountered, an 0 if not.

insects, spiders, harvestmen, idopods and snails) and to order (pseudo-scorpions, myriapods and annelids). Table 2 is a list by community of taxa of invertebrate animals found.

Since plants and animals are studied here at different taxonomic levels, certain assumptions are made in order to compare their insular or seasonal differences and to compare correlations between them and other parameters. These assumptions are discussed in the Analyses section of this report. If these assumptions hold, comparative results are not altered by this difference in taxonomic levels.

### Sampling Visits

Data were collected from each community three times during the summer of 1972. Each visit lasted about a week and was separated from the previous or next visit by about a month. The schedule for these visits is shown in Table 3.

Invertebrates were collected during Visit I and Visit II. Plant data were collected during all three visits, but were complete only for Visit III. Incomplete plant data of Visits I and II, compared sub-plot by sub-plot, were highly consistent between these visits and highly consistent with analogous data of Visit III, indicating that the sampled plant communities were constant throughout the period of study. Spring ephemerals had apparently disappeared before the beginning of the study. All subsequent analyses included animal data from Visits I and II separately and assumed plant data of Visit III to be identical for the first two visits.

Table 2. List of Invertebrate Animal Taxa, Food Habits Ranking, and Occurrences by Community and Visit.

TAXA	B	T	D	MI	MII	NBI	NBII	LI	LII	SMI	SMII
<u>INSECTA</u>											
Thysanura											
Machilidae	2	D	3	0	0	X	0	0	0	0	0
Ephemeroptera											
Caenidae	3	H	2	0	0	0	X	0	0	0	0
Orthoptera											
Tettigoniidae	3	H	2	X	0	X	0	0	0	0	0
Gryllacrididae	3	H	2	X	X	X	X	X	X	X	X
Gryllidae	3	H	2	X	X	X	X	X	X	0	X
Blattidae	3	D	1	0	X	0	0	0	0	0	0
Thysanoptera											
Thripidae	1	H	3	0	0	0	0	0	X	X	0
Ploethripidae	1	D	3	0	0	0	0	X	X	0	X
Hemiptera											
Miridae	1	H	3	X	X	X	X	0	X	X	X
Nabidae	1	C	3	X	X	0	X	0	0	0	0
Reduviidae	2	C	3	0	X	X	0	0	0	0	0
Tingidae	2	H	3	X	0	X	X	0	0	0	0
Aradidae	2	D	3	0	0	0	0	0	X	0	0
Pentatomidae	2	C	2	0	X	X	0	X	X	0	0
Homoptera											
Membracidae	1	H	3	0	X	0	X	X	0	0	0
Cicadellidae	1	H	3	X	X	X	X	X	X	X	X
Cercopidae	1	H	3	X	X	0	X	0	0	0	0
Fulgoridae	1	H	3	0	X	0	0	0	0	0	0
Aleyrodidae	2	H	3	0	X	0	0	0	X	0	0
Aphidae	1	H	3	X	X	X	X	0	X	0	0
Neuroptera											
Chrysopidae	2	C	3	0	0	0	0	0	0	0	X
Coleoptera											
Carabidae	2	C	3	X	X	X	X	X	X	X	X
Histeridae	1	C	3	X	0	0	0	0	0	0	0
Leptinidae	1	C	3	0	0	0	0	0	0	X	0
Ptiliidae	2	H	3	0	0	0	0	0	0	X	0
Leiodidae	2	D	3	0	X	0	0	0	0	0	0
Leptodiridae	3	D	3	0	0	0	0	0	0	0	X
Silphidae	2	D	2	0	0	0	0	0	0	X	X
Scaphidiidae	3	D	3	0	0	0	0	0	0	X	0
Staphilinidae	3	C	1	X	X	X	X	X	X	X	X
Orthoperidae	2	D	3	0	0	0	0	0	0	X	0
Cantharidae	3	C	3	0	0	0	0	X	0	0	X
Lampyridae	2	C	3	0	X	0	0	X	0	0	0
Lycidae	2	D	2	0	0	0	0	0	0	X	0
Cisidae	3	D	3	0	0	X	0	0	0	0	0
Cleridae	1	C	3	0	0	0	0	0	0	X	0
Elateridae	2	H	2	X	X	0	X	0	X	0	0
Eucnemidae	2	C	3	0	0	0	0	0	X	0	0
Buprestidae	2	D	3	0	0	X	0	0	0	0	0



Table 2. Continued

TAXA	B	T	D	MI	MII	NBI	NBII	LI	LII	SMI	SMII
Coleoptera, cont.											
Dascillidae	1	H	3	0	0	0	X	0	0	0	0
Byrrhidae	omit			0	0	0	0	0	0	X	0
Cucujidae	2	C	3	0	X	0	0	0	0	0	0
Nitidulidae	1	H	3	X	X	X	X	X	X	X	X
Lathridiidae	1	D	3	0	0	0	0	0	0	0	X
Endomychidae	2	D	3	0	0	X	X	0	0	0	0
Anthicidae	2	H	3	X	0	0	X	X	X	0	X
Pyrochroidae	2	D	2	0	0	0	0	X	0	0	0
Tenebrionidae	3	H	3	X	0	X	0	0	X	0	0
Lagriidae	3	D	2	0	0	0	X	0	0	0	0
Anobiidae	2	D	3	0	0	0	X	0	0	0	0
Scarabaeidae	3	D	3	X	X	0	X	X	X	X	X
Chrysomelidae	1	H	3	X	X	X	X	0	0	0	0
Bruchidae	1	H	3	0	0	X	0	0	X	0	0
Curculionidae	2	H	3	X	X	X	X	X	X	0	0
Scolytidae	1	D	3	0	0	X	0	0	0	0	0
Mecoptera											
Bittacidae	3	C	2	X	0	0	0	0	0	0	0
Trichoptera	omit			0	0	X	X	0	0	0	0
Lepidoptera											
Noctuidae	1	H	3	X	0	0	0	0	0	0	0
Liparidae	3	H	3	0	0	X	0	0	0	0	0
Pyralidae	1	H	3	0	0	0	0	0	0	X	0
Tortricidae	2	H	3	0	0	X	0	0	X	0	0
Gelechiidae	1	H	3	0	0	0	X	0	X	0	X
Diptera											
Tipulidae	2	D	2	X	0	X	0	X	X	X	0
Psychodidae	2	D	3	0	0	0	X	0	0	X	0
Culicidae	3	D	2	X	0	0	X	0	0	X	0
Ceratopogonidae	1	C	2	0	X	X	X	0	X	X	X
Chironomidae	3	D	3	X	X	X	X	X	X	X	X
Anisopodidae	3	D	3	0	0	0	0	0	0	X	0
Mycetophylidae	3	D	3	X	0	0	0	X	X	0	X
Sciaridae	3	D	3	X	X	X	X	X	X	X	X
Cecidomyiidae	1	H	3	0	X	0	X	0	X	X	X
Xylomyiidae	omit			0	0	X	0	0	0	0	0
Stratiomyiidae	3	D	2	0	X	X	0	0	0	0	X
Rhagionidae	3	C	3	X	0	0	0	0	X	0	0
Asilidae	3	C	3	0	0	0	X	0	0	0	0
Empididae	2	C	3	X	0	0	0	X	X	X	X
Dolychopodidae	2	C	3	X	X	0	0	X	X	X	X
Phoridae	2	D	3	X	X	X	X	X	X	X	X
Syrphidae	1	C	2	0	0	0	X	0	0	0	0
Conopidae	2	C	3	0	X	0	0	0	0	0	0
Otididae	2	D	3	X	0	X	0	0	0	0	0
Sciomyzidae	1	C	3	0	0	0	0	X	X	X	X
Lauxaniidae	2	D	3	0	0	X	0	X	X	X	X
Piophilidae	2	D	3	0	0	X	0	X	0	0	X

Table 2. Continued.

TAXA	B	T	D	MI	MII	NBI	NBII	LI	LII	SMI	SMII
Diptera cont.											
Lonchaeidae	3	D	2	0	0	X	0	0	0	0	0
Sphaeroceridae	3	D	3	X	X	X	X	0	X	X	X
Drosophilidae	2	D	3	0	0	X	X	X	X	X	X
Chloropidae	1	H	3	X	X	X	X	X	X	X	X
Agromyzidae	1	H	3	0	0	0	0	0	X	X	0
Heliomyzidae	3	D	3	0	0	X	0	0	0	X	X
Anthomyiidae	2	H	3	0	0	0	0	0	X	0	0
Muscidae	3	D	3	X	X	0	X	0	X	X	X
Calliphoridae	3	D	3	X	0	0	0	0	0	0	0
Tachinidae	1	C	3	0	X	0	X	X	0	X	0
Siphonaptera											
Leptopsyllidae	1	C	2	0	0	X	0	0	0	0	0
Hymenoptera											
Braconidoidea	1	C	3	X	X	X	X	X	X	X	X
Ichneumonidae	1	C	3	X	X	X	0	0	X	0	0
Mymaridae	1	C	3	X	0	0	0	0	0	X	0
Eulophidae	2	C	3	0	0	0	X	X	X	0	0
Encritidae	1	C	3	0	0	0	0	0	0	X	0
Eupelmidae	3	C	3	0	0	X	X	0	0	0	0
Eurytomidae	2	H	3	0	0	X	0	0	0	0	0
Chalcidae	1	C	3	0	0	0	0	0	X	X	0
Cynipidae	1	H	3	0	0	0	X	0	X	X	X
Roproniidae	1	C	3	0	X	0	X	0	0	0	0
Proctotrupidae	1	C	3	0	0	X	0	X	0	0	0
Ceraphronidae	2	C	3	X	X	X	X	X	X	0	X
Diapriidae	1	C	3	X	X	X	X	X	X	0	X
Scelionidae	1	C	3	X	X	X	X	X	X	0	0
Platygasteridae	1	C	3	0	0	X	X	0	0	0	0
Dryinidae	1	C	3	X	X	0	X	X	0	0	0
Formicidae	3	C	1	X	X	X	X	X	X	X	X
Sphecidae	1	C	3	X	0	X	0	0	0	0	0
Halictidae	2	H	3	0	0	0	X	0	0	0	0
ARACHNIDA											
Chelonethida	3	C	3	X	0	X	0	0	0	0	0
Opiliones											
Phalangiidae	3	C	1	X	X	X	X	X	X	X	X
Araneae											
Dyctinidae	2	C	3	0	0	0	0	0	0	0	X
Theridiidae	2	C	3	X	0	0	0	0	0	0	0
Lyniphiidae	2	C	3	X	0	X	0	0	X	X	X
Micryphantidae	2	C	3	0	0	X	X	X	X	X	0
Araneidae	2	C	3	X	X	X	X	X	X	0	0
Agelenidae	3	C	3	0	0	0	0	0	0	X	X
Hahniidae	3	C	3	X	0	X	X	X	X	X	X
Lycosidae	3	C	3	X	X	X	X	X	X	X	0
Gnaphosidae	3	C	3	X	X	X	X	X	X	0	X
Clubionidae	3	C	3	X	X	0	0	0	0	0	0
Thomisidae	3	C	3	X	X	X	0	X	X	0	X
Salticidae	3	C	3	X	X	X	0	X	0	X	0

Table 2. Continued.

TAXA	B	T	D	MI	MII	NBI	NBII	LI	LII	SMI	SMII
<u>CRUSTACEA</u>											
<u>Isopoda</u>											
Armadillidiidae	3	H	2	0	0	X	X	0	0	0	0
Porcellionidae	3	D	3	X	X	X	X	X	X	0	0
Trichoniscidae	3	D	3	0	0	X	0	0	X	0	X
<u>DIPLOPODA</u>											
Polydesmida	3	D	3	0	X	0	0	X	X	0	0
Julida	3	D	3	X	X	X	X	X	X	X	X
<u>CHILOPODA</u>											
Watobiida	3	C	3	X	0	X	0	X	X	X	X
Geophilida	3	C	3	0	0	0	0	0	X	0	0
<u>OLIGOCHAETA</u>											
Opisthopora	3	D	3	X	X	X	0	0	X	X	X
Hirudinea	2	C	3	0	0	X	0	0	0	0	0
<u>PULMONATA</u>											
<u>Stylomatophora</u>											
Cionellidae	3	H	2	0	0	0	0	0	0	X	0
Pupillidae	2	H	2	X	0	X	0	X	0	0	0
Succineidae	3	H	2	X	0	0	0	X	X	X	0
Endodontidae	3	H	2	X	0	0	X	X	X	0	X
Limacidae	2	H	3	X	X	X	X	X	X	X	X
Zonitidae	3	H	2	X	0	X	X	X	X	X	X
Polygiridae	3	H	2	X	0	0	0	X	0	X	X

Columns B, T, and D list the rank assigned each taxon in terms of Resource Breadth, Trophic Level, and Distinctness of Trophic Levels, respectively.

Columns MI, MII, NBI, NBII, LI, LII, SMI, and SMII indicate the communities and visits: Ohio mainland, Visit I; Ohio mainland, Visit II; Ohio island, Visit I; Ohio island, Visit II; Michigan mainland, Visit I; Michigan mainland, Visit II; Michigan island, Visit I, and Michigan island, Visit II, respectively. Under these columns is placed an X if the taxon was encountered, a 0 if not.

Table 3

## SCHEDULE OF VISITS TO THE FOUR COMMUNITIES STUDIED

Community Visited	Inclusive Dates
Marblehead	June 14 - June 22
North Bass	June 25 - July 1
Leelanau	July 5 - July 10
South Manitou	July 13 - July 18
Marblehead	July 21 - July 26
North Bass	July 29 - August 2
Leelanau	August 4 - August 10
South Manitou	August 11 - August 17
Marblehead	August 25 - August 30
North Bass	September 1 - September 6
Leelanau	September 8 - September 13
South Manitou	September 15 - September 21

## THEORETICS

### Selection of Parameters

In this section the selection of parameters is explained and the parameters are described more fully.

A food-web is a system in which taxa of plants and animals are related in web-like fashion by relationships of eating or being eaten (trophic connections), and in which the web is given directional pattern by the movement of energy among trophic levels (see Fig. 8). This system may be viewed in many different ways. In the present study, a food-web is viewed as a system which contains three components: (1) the taxa of organisms, (2) the trophic connections among the taxa, and (3) the trophic levels. Several kinds of measurements can be made on these three components. Three of these are the following: (1) the number of units comprising a component (i.e., the number of taxa, the number of trophic connections per taxon, or the number of trophic levels), (2) the relative or proportional sizes of units comprising a component, and (3) the distinguishability of units comprising a component.

A total of nine measurements results when these three kinds of measurements are made on each of the three components of the food-web system (Table 4). Biologically, these nine measurements are the following:

Number of Taxa (e.g., number of species, number of families)

Evenness of Taxa (a measure of the relative abundances of the taxa)

Resource Overlap (degree of overlap in resource use is a measure of distinguishability of taxa in the trophic sense)

Resource Breadth (the number of food sources used by the consumer taxa)

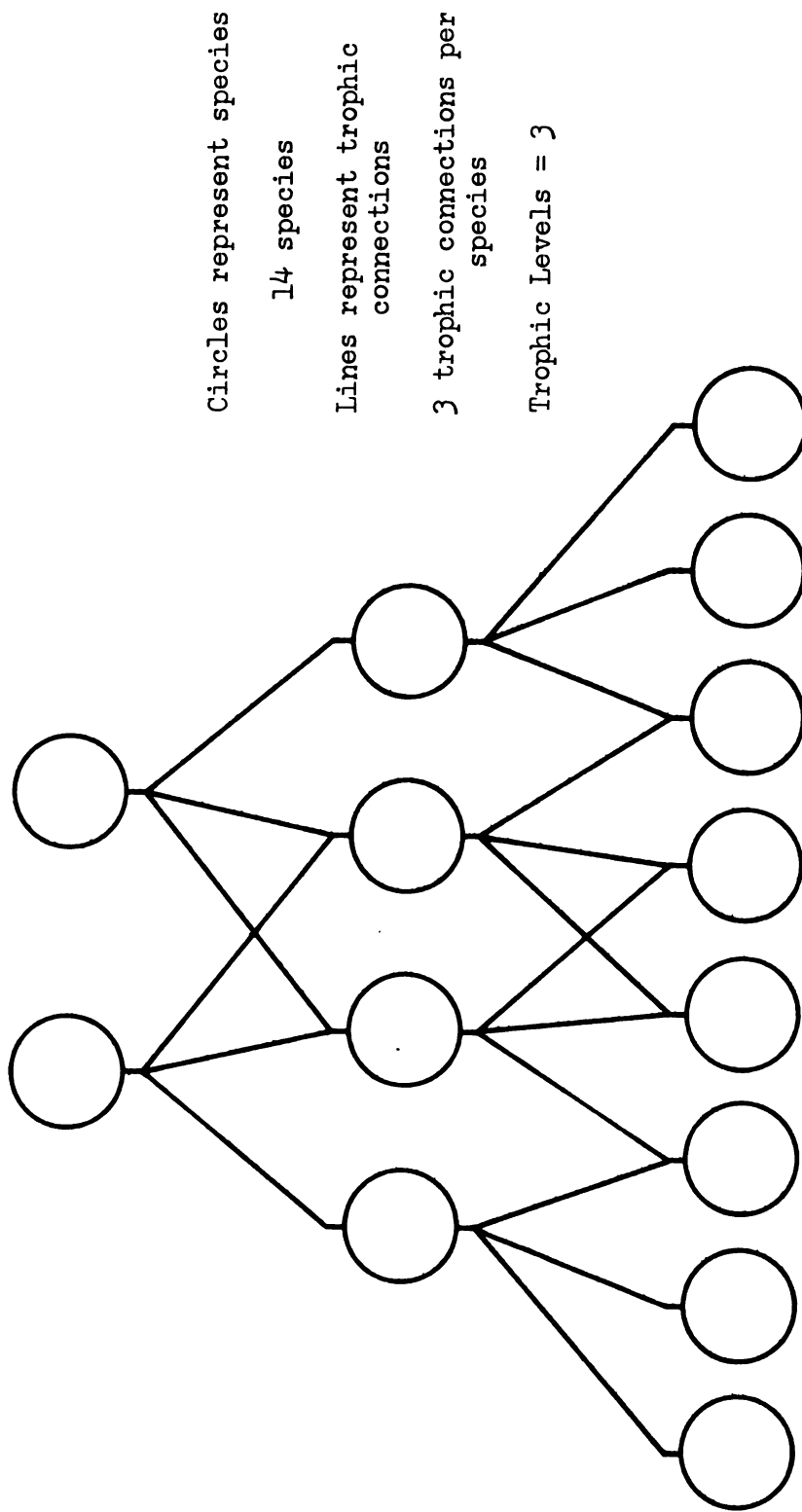


Figure 8. Diagram of a Food-Web.

Table 4. Three Food-Web Components, Rows, and Three Kinds of Measurements, Columns, and the Resulting Nine Measurements.

	NUMBER	RELATIVE SIZES	DISTINCTNESS
TAXA	NUMBER OF TAXA	EVENNESS OF TAXA	RESOURCE OVERLAP
TROPHIC CONNECTIONS	RESOURCE BREADTH	RESOURCE BREADTH	SELECTIVITY OF FEEDING
TROPHIC LEVELS	NUMBER OF TROPHIC LEVELS	EVENNESS OF TROPHIC LEVELS	DISTINCTNESS OF TROPHIC LEVELS

Resource Breadth (the relative proportions of those food sources used  
by the consumer taxa)

Selectivity of Feeding (deviation of feeding by consumer taxa from  
random strategy is a measure of distinguishability of trophic  
connections per taxon)

Number of Trophic Levels

Evenness of Trophic Levels (relative number of taxa, or of individual  
organisms, per trophic level)

Distinctness of Trophic Levels (the degree to which consumer taxa  
selectively distinguish lower trophic levels in feeding)

Five of the above ecological parameters investigated more fully in  
this study, and already mentioned in the Introduction of this report, are

Number of Taxa

Evenness of Taxa

Resource Breadth

Evenness of Trophic Levels

Distinctness of Trophic Levels

The two parts of Resource Breadth, above, have been treated in combined  
fashion by Colwell and Futuyma (1971) and by Pielou (1972) and are also  
combined in the present study. Of the three parameters not investigated  
in this study, Number of Trophic Levels does not differ among the  
communities studied, and the logistics and time involved in measuring  
Resource Overlap and Selectivity of Feeding were incompatible with the  
resources of this study.



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### Expected Effects of Insularity and Seasonality

In accordance with the first goal of this study, this section explores, by review of the pertinent literature, the expected influences of insularity and seasonality on the five parameters investigated in this study. The five parameters are treated individually below.

Number of Taxa -- MacArthur and Wilson (1963) have proposed a model to explain the paucity of species on islands relative to mainlands in terms of island area and distance from mainland. This model has been strongly supported by experimental test (Wilson and Simberloff, 1969). Other factors also found to affect species numbers on islands are island elevation (birds, Hamilton and Armstrong, 1965), densities of mainland source populations (small mammals, McPherson and Krull, 1972), number of resource (plant) species (birds, Power, 1972) and evolutionary adaptation of species to the island environment and to each other (ants, Wilson and Taylor, 1967). In all cases, however, islands are expected to have fewer taxa than adjacent and similar mainland areas, and the same is predicted in the present study.

Few studies indicate a consistent change in number of taxa during the summer growing season. A study by Hurd et al. (1971) suggests that numbers of herbivore insect taxa increase during this season in unused hay fields. Pulliam et al. (1968) indicate that number of spider species increases from five to twelve in a field of millet between July 9 and September 2, 1966. Thus it may be predicted, although with little confidence, that in this study Number of Taxa will increase during the period of study.

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Evenness of Taxa -- The analyses of Preston (1962, a, b) suggest the selective loss of rare species on islands, which would result in increased Evenness of Taxa on islands. MacArthur (1969a) has suggested that where there are many species, as in the tropics, relative abundances would approach equality, and therefore evenness would be high. It can be predicted only tentatively in the present study that Evenness of Taxa will be larger on islands than on mainlands.

Pulliam, Odum and Barrett (1968) measured Evenness of Taxa of various arthropods during the growing season in a field of millet. Although the evenness of spider species tended to increase, that of homopteran species and carnivorous hemipteran species tended to decrease over time. As discussed above, Evenness of Taxa may decrease with increased Number of Taxa on the mainland, and we have predicted an increase in Number of Taxa during the period of study. It may again be predicted, with little confidence, that Evenness of Taxa, in the present study, will decrease during the summer growing season.

Resource Breadth -- Several investigators have shown that birds utilize a wider variety of resources on islands than on mainlands (Crowell, 1961, 1962; Grant, 1966, 1968; Sheppard, Klopfer and Oelke, 1968; Keast, 1970; Morse, 1971; MacArthur, Diamond and Karr, 1972). This phenomenon has been termed evolutionary (or ecological) release (MacArthur and Wilson, 1967). Ricklefs and Cox (1972) suggest that this expansion of Resource Breadth is an early part of a more general cycle of invasion, adaptation, and extinction of taxa on islands. In addition, Williams (1969) has shown that colonizing anoline lizards tend to be of "versatile" species and may undergo ecological release. These reports, although dealing primarily

with birds, suggest the prediction that Resource Breadth of invertebrates in the present study will be higher on islands than on mainlands.

The literature reviewed provides no evidence regarding any patterns of differences in Resource Breadth during any season.

Evenness of Trophic Levels -- Again, the literature reviewed provides no evidence regarding any patterns of differences in Evenness of Trophic Levels between islands and mainlands.

In a study of insect trophic diversity in salt marsh communities, Cameron (1972) has shown that, during a single year, the diversities of herbivores, saprovores and predators are more nearly equal in June and July than in August and September. These results suggest the prediction, in the present study, that Evenness of Trophic Levels will decrease during the period of study.

Distinctness of Trophic Levels -- Due to the total inadequacy of the reviewed literature regarding Distinctness of Trophic Levels, no a priori predictions of insular or seasonal effects on this parameter may be made, but must await the outcome of the present study.

#### Models of Relationships among Parameters

Free-Body Model Concept -- As a first step in inferring expected relationships among these parameters, each of them was investigated, independently, by survey of the ecological literature. The information from this survey was collated into a diagramatic compartment model for each parameter independently. Each such model describes expected cause-effect relationships between one of the five parameters and any other ecological parameters that presumably influences it. These individual

models are analogous to free-body models of systems science (see Caswell, Koenig, Resh and Ross, 1972), and are termed free-body models in the present study. Development of each free-body model independently of the others avoids the pitfall of defining relationships among those parameters studied as a necessary and sufficient set of relationships, even though parameters external to the system may exert an important influence on one or more of the parameters of the system. These five free-body models can be combined in a diagrammatic compartment model of expected relationships among the parameters as a system, which is herein called a system model.

The information obtained from the literature survey was sometimes clearly and concisely presented in the original source. At other times it was obtained by examination of data or conclusions of the source article from the viewpoint of the present study. This information was used in this report if it logically led to a hypothesis of relationship between any two ecological parameters and linked either of them directly or indirectly to any of the five parameters primarily investigated in this report. Information surveyed and found unsuitable is not referenced.

The following paragraphs are descriptions of the free-body models and the system model. References are not included in these descriptions for the sake of clarity. Rather, they are listed in Tables 5-9. In each of these tables, the parameters listed on the left, heading the rows, are hypothesized to directly affect those parameters at the top of the table, heading the columns. The cell entries list the references used to hypothesize this effect.

Statements in these descriptions must be viewed as reasonable hypotheses, not as clearly shown facts. Even though the writing appears factual, it does so for the sake of brevity only. Although parameters of

importance may have been omitted from these free-body models, and they may contain some duplication, they represent the most parsimonious and complete models that this author has been able to infer from the literature reviewed.

Number of Taxa -- Figure 9 illustrates the schematic compartment model that has been developed as the free-body model for Number of Taxa.

References are listed in Table 5. This model is relatively complex: It consists of five hierarchic levels of a total of thirty-six parameters and includes four instances of feed-back. This complexity may be in part due to the large volume of literature reviewed: seventy-two published articles are used to generate this model. The four parameters most directly related to Number of Taxa (see Figure 9) each represent some general effect achieved by any of a variety of mechanisms. These mechanisms plus other "general-effect" parameters constitute the parameters of the next level removed in this hierarchy from Number of Taxa. This pattern continues until the five levels of the hierarchy are completed.

Beginning with the first parameter in Figure 9 affecting Number of Taxa, the Number of Taxa estimated by a sample is directly proportional to the size of the sample, is increased by inclusion of ecotones in the sample or by lack of discreteness of communities sampled and by relatively great differences among communities sampled.

Number of Taxa will be decreased by Extinction and increased by speciation and by Immigration.

The probability of extinction of species in a community is increased if the Minimum Density needed for reproduction by the constituent populations is increased, is increased by periodic small scale perturbations of the environment, is increased by Competition, but is decreased by Adaptation.

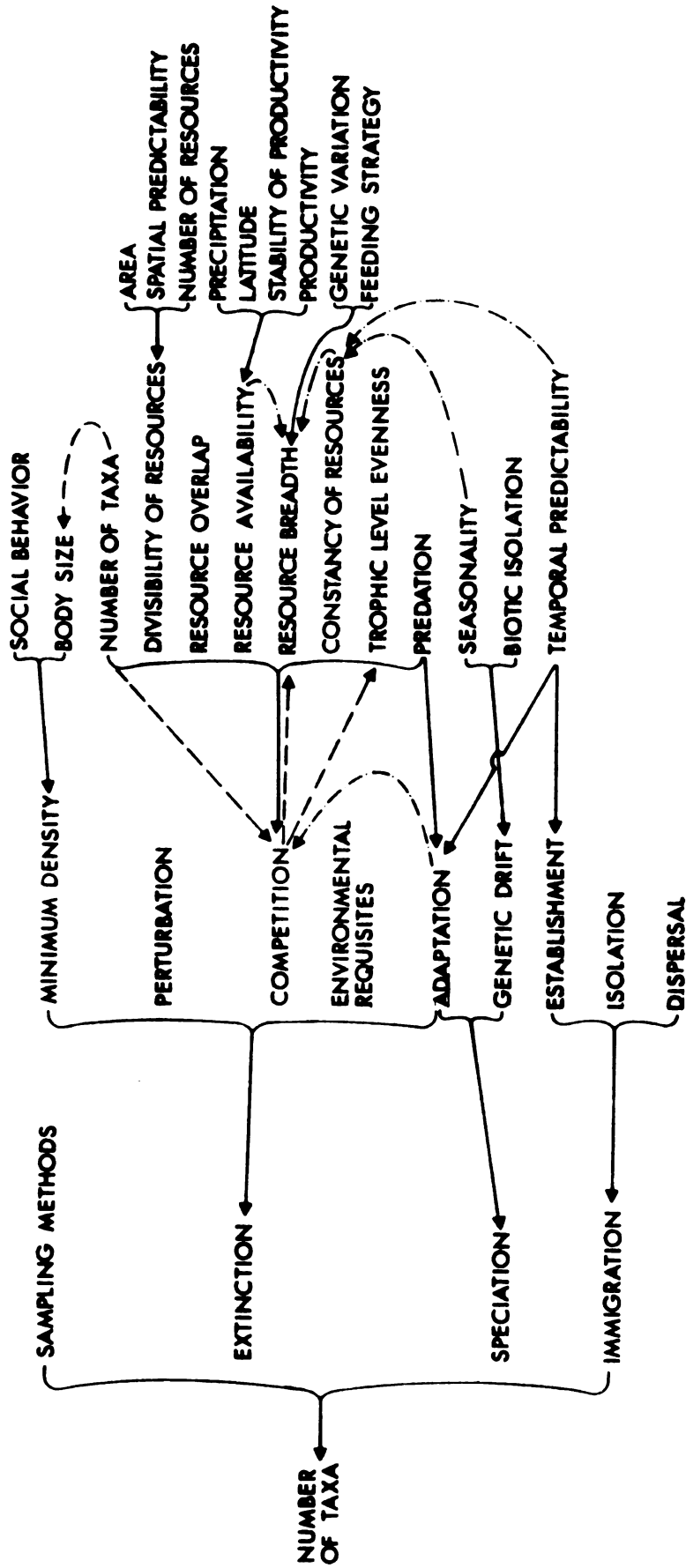


Figure 9. Free-Body Model of Number of Taxa.



Table 5. Table of References Relating Ecological Parameters that Lead to Free-Body Model of Number of Taxa

	NUMBER OF TAXA	EXTINCTION	SPECIATION	IMMIGRATION
Sampling Methods	Kilburn, 1966 Margalef, 1967 Johnson and Raven 1970 M'Closkey, 1972 Janzen and Schoener, 1968 Orians, 1969			
Extinction	Connell and Orias, 1964 MacArthur and Wilson, 1963 Williams, 1969			
Speciation	Connell and Orias, 1964 Federov, 1966 Johnson and Raven, 1970 MacArthur, 1969a Pianka, 1966 Vuilleumier, 1972			
Immigration	Johnson and Raven 1970 MacArthur, Diamond and Karr, 1972 MacArthur and Wilson, 1963			

Table 5. Continued

	NUMBER OF TAXA	EXTINCTION	SPECIATION	IMMIGRATION
Immigration (Continued)	Pulliam, Odum and Barrett, 1968 Ricklefs and Cox, 1972			
Minimum Density		Johnson and Raven, 1970 McPherson and Krull, 1972 Phillip, 1957 Preston, 1962b		
Perturbation		Auclair and Goff, 1971 Hurlbert, Mulla and Willson, 1972 Johnson, 1970 Loucks, 1970 Malone, 1972		
Competition		Arnold, 1972 Auclair and Goff, 1972 Baker, 1971 Cameron, 1972 Crowell, 1962 Federov, 1966 Grant, 1966 Keast, 1970 MacArthur, 1965, 1969a, 1969b, 1970		



Table 5. Continued

	NUMBER OF TAXA	EXTINCTION	SPECIATION	IMMIGRATION
Competition (Continued)		<p>MacArthur, Diamond and Karr, 1972</p> <p>MacArthur and Wilson, 1967</p> <p>Odum, 1969</p> <p>Paine, 1966</p> <p>Pielou, 1966</p> <p>Porter, 1972a</p> <p>Pulliam, Odum and Barrett, 1968</p> <p>Ricklefs and Cox, 1972</p> <p>Schoener, 1969</p> <p>Terborgh, 1971</p> <p>Vandermeer, 1970</p> <p>Williams, 1969</p>		
Adaptation		<p>Cameron, 1972</p> <p>Federof, 1966</p> <p>Futuyama, 1973</p> <p>MacArthur, 1970</p> <p>MacArthur and Wilson, 1967</p> <p>Pianka, 1966</p> <p>Ricklefs and Cox, 1972</p> <p>Simberloff, 1969</p> <p>Williams, 1969</p>	<p>Cameron, 1972</p> <p>Pianka, 1966</p> <p>Ricklefs and Cox, 1972</p>	

Table 5. Continued

	NUMBER OF TAXA	EXTINCTION	SPECIATION	IMMIGRATION
Genetic Drift			Federov, 1966 MacArthur and Wilson, 1967	
Establishment				Hamilton and Armstrong, 1965 Johnson, Mason and Raven, 1968 Kohn, 1967 MacArthur and Wilson, 1963 Power, 1972 Ricklefs and Cox, 1972 Simberloff, 1969a
Dispersal				Beer, Lukens and Olsen, 1954 Simberloff, 1969a Williams, 1969

Table 5. Continued

	MINIMUM DENSITY	COMPETITION	ADAPTATION	GENETIC DRIFT	ESTABLISHMENT
Social Behavior	Phillip, 1957				
Body Size	Crowell, 1962 Leigh, 1965 MacArthur, Diamond and Karr, 1972 MacArthur, MacArthur, MacArthur and MacArthur, 1973				
Number of Taxa		Arnold, 1972 Baker, 1971 Crowell, 1962 Grant, 1966 MacArthur, 1965, 1969a Odum, 1969 Paine, 1966 Ricklefs and Cox, 1972 Schoener, 1969 Vandermeer, 1970 Williams, 1969			
Divisibility of Resources		Baker, 1971 Connell and Orias, 1964			

Table 5. Continued

	MINIMUM DENSITY	COMPETITION	ADAPTATION	GENETIC DRIFT	ESTABLISHMENT
Divisibility of Resources (Continued)		Hutchinson, 1959 Klopfer and MacArthur, 1961 MacArthur, 1965 MacArthur and Recher, 1966			
Resource Overlap		Klopfer and MacArthur, 1961 MacArthur, 1965 MacArthur and Recher, 1966 Pulliam, Odum and Barrett, 1968			
Resource Availability		Cameron, 1972 Connell and Orias, 1964 Fleming, 1973b Heatwole and Levins, 1973 Hutchinson, 1959 Leigh, 1965 MacArthur, 1970 Mackay and Kalf, 1969 Paine, 1966 Pearson, 1971 Planka, 1966, 1967 Teal, 1962 Vandermeer, 1970			

Table 5. Continued

	MINIMUM DENSITY	COMPETITION	ADAPTATION	GENETIC DRIFT	ESTABLISHMENT
Resource Breadth		Baker, 1971 Grant, 1966 MacArthur and Levins, 1964, 1967 Pianka, 1969 Ricklefs and Cox, 1972 Williams, 1969			
Constancy of Resources		Cameron, 1972 Fleming, 1973b MacArthur, 1969a, 1969b, 1970 MacArthur, Diamond and Karr, 1972 Margalef, 1967 Orians, 1969 Paine, 1969 Pianka, 1966			
Trophic Level Evenness and Predation		Arnold, 1972 Auclair and Goff, 1971 Garfinkel and Sack, 1964 Heatwole and Levins, 1973 Hurlbert, Mulla and Willson, 1972			



Table 5. Continued

	MINIMUM DENSITY	COMPETITION	ADAPTATION	GENETIC DRIFT	ESTABLISHMENT
Trophic Level Evenness and Predation (Continued)		Hurlbert, Zedler and Fairbanks, 1972 Janzen, 1970 Paine, 1966 Parrish and Saila, 1970 Porter, 1972a Rosenzweig, 1973			
Competition, Predation, and Temporal Predictability			Levins, 1968 Levinton, 1972 MacArthur and Levins, 1964, 1967 Pianka, 1966 Slobodkin and Sanders, 1969		
Biotic Isolation and Seasonality				Federov, 1966 MacArthur and Wilson, 1967	
Temporal Predictability					Levins, 1968 Levinton, 1972 MacArthur and Levins, 1964, 1967

Table 5. Continued

Number of Taxa	Schoener, 1969	BODY SIZE	DIVISIBILITY OF RESOURCES	RESOURCE AVAILABILITY	RESOURCE BREADTH	CONSTANCY OF RESOURCES
Area			Beer, Ludens and Olsen, 1954 Grant, 1966 Hamilton and Armstrong, 1965 Hamilton, Barth and Rubinoft, 1964 Hutchinson, 1959 Johnson, Mason and Raven, 1968 Johnson and Mason, 1970 Kilburn, 1966 MacArthur, 1965 MacArthur and Wilson, 1963 McPherson and Krull, 1972 Power, 1972 Preston, 1962b Ricklefs and Cox, 1972 Simberloff, 1969a Vuilleumier, 1972 Williams, 1969			

Table 5. Continued

	BODY SIZE	DIVISIBILITY OF RESOURCES	RESOURCE AVAILABILITY	RESOURCE BREADTH	CONSTANCY OF RESOURCES
Spatial Predictability		<p>Dwyer, 1973</p> <p>Fleming, 1973b</p> <p>Hamilton and Armstrong, 1965</p> <p>Hutchinson, 1959</p> <p>Johnson, 1970</p> <p>Johnson, Mason and Raven, 1968</p> <p>Johnson and Raven, 1970</p> <p>Kohn, 1967</p> <p>Loucks, 1970</p> <p>MacArthur, 1964, 1965</p> <p>Mackay and Kalf, 1969</p> <p>Murdoch, Evans and Peterson, 1972</p> <p>Orians, 1969</p> <p>Pearson, 1971</p> <p>Pianka, 1966, 1967, 1969</p> <p>Porter, 1972b</p> <p>Sheldon, 1968</p> <p>Terborgh, 1971</p> <p>Whiteside and Harmsworth, 1967</p>			

Table 5. Continued

	BODY SIZE	DIVISIBILITY OF RESOURCES	RESOURCE AVAILABILITY	RESOURCE BREADTH	CONSTANCY OF RESOURCES
Number of Resources		Arnold, 1972 Baker, 1971 Hairston, <u>et al.</u> , 1968 MacArthur, 1969a, 1969b Murdoch, Evans and Peterson, 1972 Orians, 1969 Power, 1972			
Precipitation			Johnson, Mason and Raven, 1968 Power, 1972		
Latitude			Malone, 1972 Pianka, 1967		
Stability of Productivity			Cameron, 1972 Fleming, 1973b MacArthur, 1970 MacArthur, Diamond and Karr, 1972 Margalef, 1967 Orians, 1969 Paine, 1966 Pianka, 1966		

Table 5. Continued

	BODY SIZE	DIVISIBILITY OF RESOURCES	RESOURCE AVAILABILITY	RESOURCE BREADTH	CONSTANCY OF RESOURCES
Productivity			Connell and Orias, 1964 Hurd, Mellinger and McNaughton, 1971 MacArthur, 1965, 1970 MacArthur, Diamond and Karr, 1972 Paine, 1966 Pianka, 1966, 1967 but see Whiteside and Harmsworth, 1967		
Genetic Variation				(see Table 7)	
Feeding Strategy				(see Table 7)	
Resource Availability				(see Table 7)	
Seasonality					Federov, 1966 MacArthur and Wilson, 1967

Table 5. Continued

	BODY SIZE	DIVISIBILITY OF RESOURCES	RESOURCE AVAILABILITY	RESOURCE BREADTH	CONSTANCY OF RESOURCES
Temporal Predictability					Levins, 1968 MacArthur and Levins, 1964, 1967 Pianka, 1966 Slobodkin and Sanders, 1969

Adaptation may also lead to Speciation, or Speciation may come about by Genetic Drift.

Establishment may be considered a necessary component of Immigration, while enhanced dispersal capabilities of species may increase Immigration.

Minimum Density needed for reproduction of a population is decreased by gregarious Social Behavior and, for widely ranging rare, large, or competing species, may not be reached if area is restricted.

Review of the literature suggests that Competition is most often used as a "general-effect" parameter, rather than a clearly defined biological parameter. It is used to categorize a variety of non-predaceous inter-species or intra-species interactions and to generalize the effects of these interactions on Extinction or Adaptation of species. The literature indicates that Competition is influenced by a large number of other parameters, (This report categorizes nine of them.) but whether all mechanisms of competition are affected by all these parameters is unclear. Competition is presumably increased by an increase in Number of Taxa. This effect represents part of a negative feed-back loop since increase in Competition in this model leads to an increase in probability of Extinction, which leads to a decrease in Number of Taxa. Increase in Number of Taxa may also lead to a decrease in Body Size, which may act as a positive feed-back loop, ultimately permitting the larger Number of Taxa. A finer Divisibility of Resources may reduce Competition, as would increased Resource Overlap and increased Resource Availability. An increase in Resource Breadth may increase Competition, while an increase in Competition may decrease Resource Breadth, forming a negative feed-back loop. As Constancy of Resource supply decreases, Competition may also be expected to decrease. Under conditions of low Trophic Level Evenness

(proportion of predator taxa is small), or when Predation in general is reduced, then Competition among the taxa preyed upon may be high. This increase in Competition is likely to reduce the Number of Taxa preyed upon, thus increasing Evenness of Trophic Levels and, relatively, increasing Predation. This set of relationships forms another negative feed-back loop.

Adaptation, somewhat like Competition, is used to categorize a variety of evolutionary processes which may reduce Competition, directly reduce the probability of Extinction, or lead to Speciation. These changes may be guided by the selective forces of Competition, Predation or by Temporal Predictability.

Genetic Drift may contribute significantly to Speciation in the absence of Seasonal rythm coupled with strong Biotic Isolation.

Divisibility of Resources may be limited by available Area, by Spatial Predictability (heterogeneity) or by Number of Resources.

Influences on Resource Breadth are discussed in the sub-section dealing with that parameter.

Evenness of Taxa -- The free-body model for Evenness of Taxa (Figure 10) is simpler than that for Number of Taxa. It consists of only three hierarchic levels of a total of fourteen parameters and includes no obvious cases of feed-back. References are listed in Table 6.

Evenness of Taxa can be under-estimated by samples so large that they compound different habitats or over-estimated by small random samples. Evenness of Taxa per unit area is decreased by any tendency of organisms to be distributed spatially in a Clumped manner, and Clumping can apparently be determined by Resource Patch Size and by gregarious



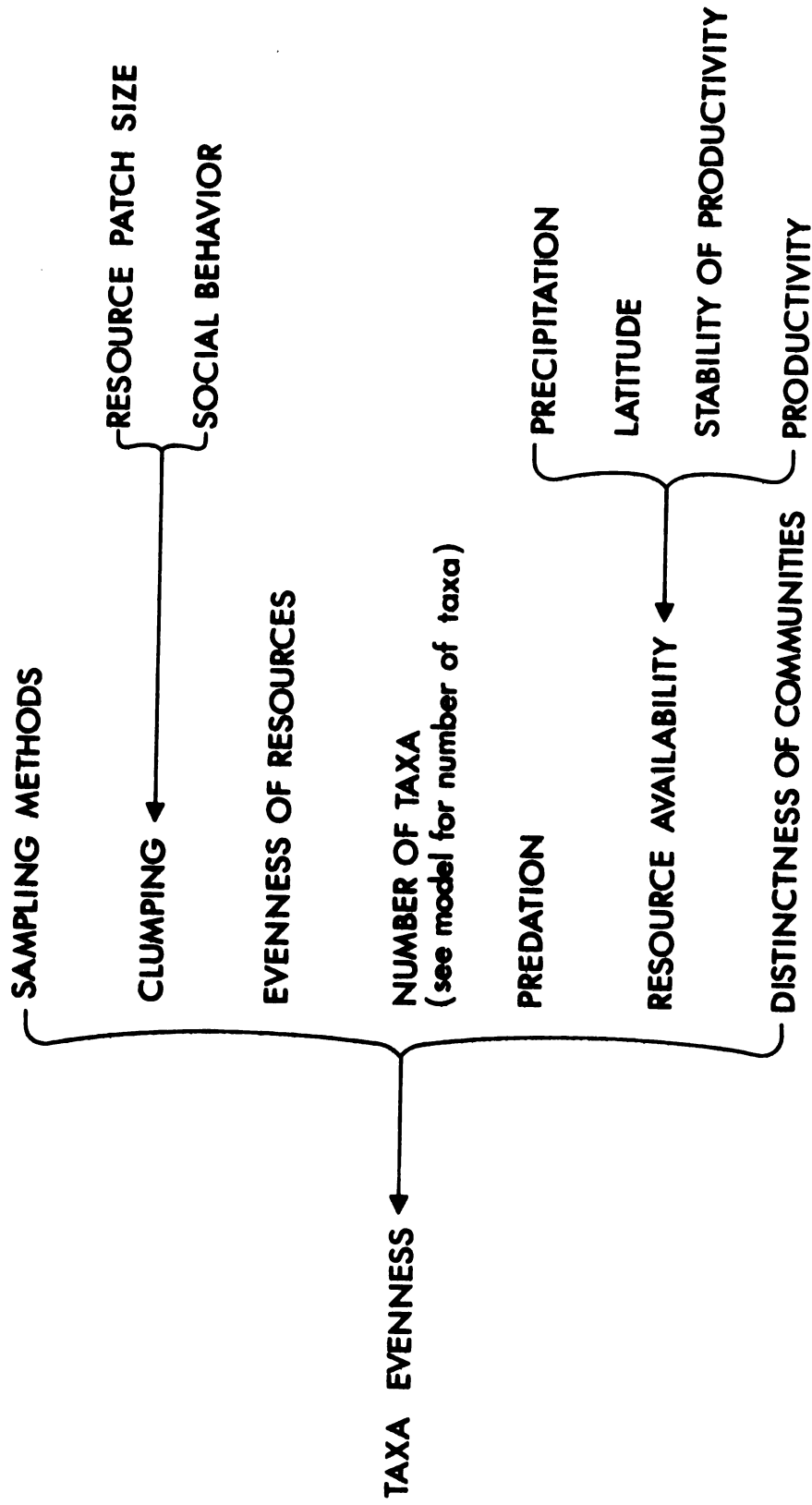


Figure 10. Free-Body Model of Evenness of Taxa.

Table 6. Table of References Relating Ecological Parameters that Lead to Free-Body Model of Evenness of Taxa.

	Taxa Evenness	Clumping	Resource Availability
Sampling Methods	MacArthur, 1965 Johnson and Raven, 1970		
Clumping	Hairston, 1959 Tramer, 1969		
Evenness of Resources	Fleming, 1973b Murdoch, Evans and Peterson, 1972		
Number of Taxa	Preston, 1962b Hairston, 1959 MacArthur, 1969a Auclair and Goff, 1971 Johnson and Raven, 1970 Murdoch, Evans and Peterson, 1972 Porter, 1972a, 1972b Reiners, Wooly and Lawrence, 1971 M'Closkey, 1972 DeBenedictis, 1973		
Predation	Porter, 1972a Ares and Leon, 1972		

Table 6. Continued

	Taxa Evenness	Clumping	Resource Availability
Resource Availability	MacArthur, 1969a Fleming, 1973a Pulliam, Odum and Barrett, 1968		
Distinctness of Communities	Preston, 1962a		
Resource Patch Size		Kricher, 1972	
Social Behavior		Kricher, 1972	
Precipitation			(see Table 5)
Latitude			(see Table 5)
Stability of Productivity			(see Table 5)
Productivity			(see Table 5)

Social Behavior and opposed by Territoriality. Two studies show or suggest a correlation between Evenness of Taxa and the Evenness of their Resources.

As Number of Taxa increases, new taxa are apparently more likely to be rare than common, decreasing Evenness of Taxa. On the other hand, the large Number of Taxa in the tropics may require that they all be about equally distributed, increasing Evenness of Taxa. Several authors indicate a positive correlation between Evenness of Taxa and either Number of Taxa or diversity. Another finds no such correlation, and still another claims that published data only indicate, biologically, a decrease in the variance of Evenness of Taxa as Number of Taxa increases. It appears logical, at this point, to hypothesize a second order relationship between Evenness of Taxa and Number of Taxa, such that, beginning with no taxa, the first few taxa added will be the more common ones, and Evenness will be high. Further taxa added will increasingly be the more rare ones, and Evenness will decrease. But at some point, addition of further taxa will require decreased abundance of the more common taxa already present, and from this point forward addition of taxa will be accompanied by increase in Evenness.

For further influences on Number of Taxa, see the sub-section and model for that parameter.

Predation by the starfish, Acanthaster, can markedly increase the Evenness of prey Taxa, coral species, presumably by preventing competitive interactions among those taxa. However in another study, Evenness of plant taxa is higher at low grazing pressure than at high grazing pressure. It appears reasonable to suggest that as intensity of predation increases

from zero Evenness also increases, until a threshold tolerance of some taxa is reached, and Evenness will then begin to decline.

Evenness of Taxa may be high in the tropics where Resource Availability is great, and Evenness of Costa Rican rodent species was low where food was limited. Others suggest that high Evenness indicates food limitation of the taxa involved. It is possible that Resource Availability influences Evenness of Taxa indirectly only by first influencing Number of Taxa.

Evenness of Taxa, computed from communities which are not Distinct, but rather continuous, may be relatively low.

Resource Breadth -- The free-body model for Resource Breadth (Fig. 11) is also relatively simple, consisting of three hierarchic levels and a total of thirteen parameters. It does, however, include two feedback loops. References are listed in Table 7.

In general, Resource Breadth should increase as Constancy of Resources decreases, and the latter may be determined by Temporal Predictability and Seasonality.

An increase in Competition, as discussed previously, may decrease Resource Breadth, while an increase in Resource Breadth may increase Competition, forming a negative feedback loop. For discussion of other influences on Competition, see discussion of free-body model for Number of Taxa.

Feeding Strategy can apparently influence Resource Breadth in various ways. MacArthur has hypothesized that searchers should be relatively more generalized than pursuers, and thus should exhibit greater Resource Breadth.

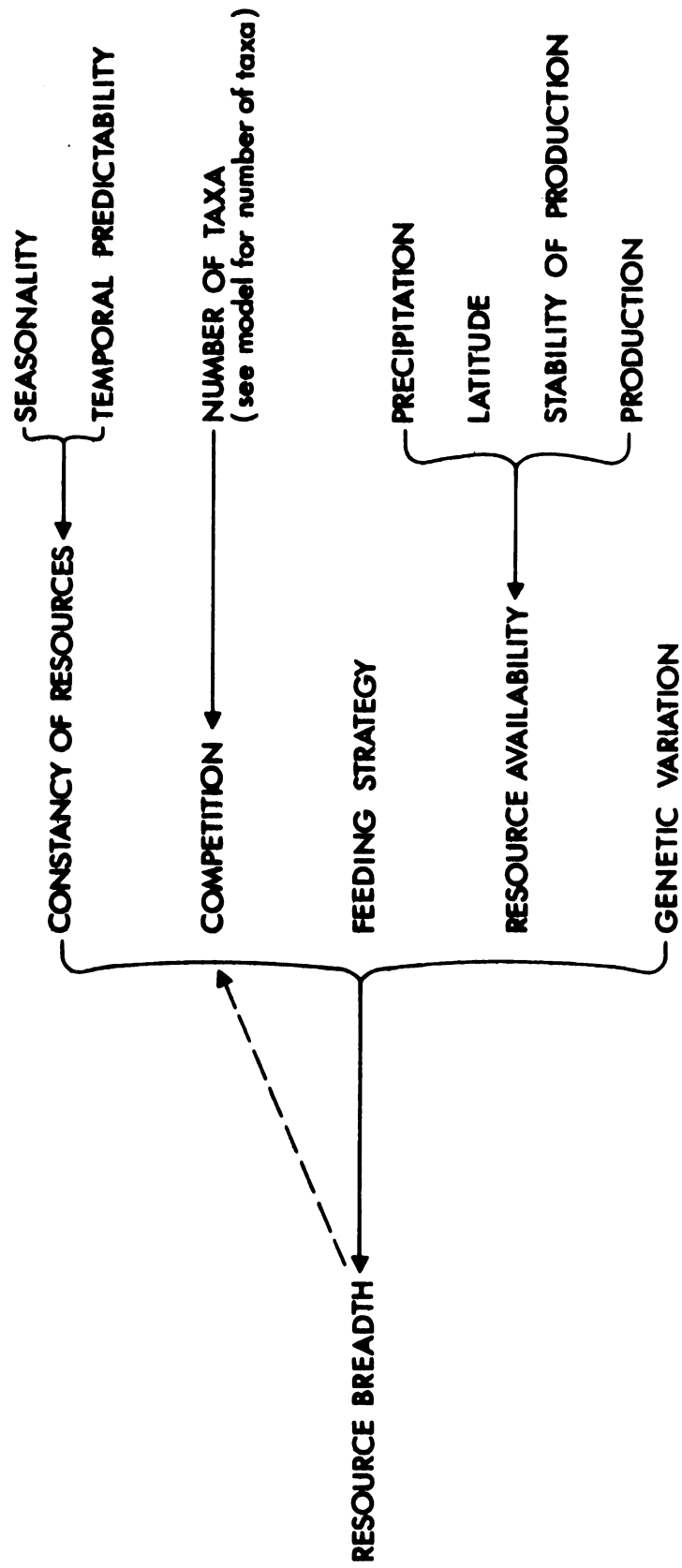


Figure 11. Free-Body Model of Resource Breadth.

Table 7. Table of References Relating Ecological Parameters that Lead to Free-Body Model of Resource Breadth.

	Resource Breadth	Constancy of Resources	Competition	Resource Availability
Constancy of Resources	Connell and Orias, 1964 MacArthur, 1970 Orias, 1969			
Competition	Crowell, 1962 Grant, 1966 Keast, 1970 MacArthur, 1965 MacArthur and Recher, 1966 MacArthur and Wilson, 1967 McPherson and Krull, 1972 Ricklefs and Cox, 1972			
Feeding Strategy	Baker, 1971 MacArthur and Levins, 1964 Schoener, 1968 MacArthur, 1964, 1972			
Resource Availability	Connell and Orias, 1964 Hutchinson, 1959			

Table 7. Continued

	Resource Breadth	Constancy of Resources	Competition	Resource Availability
Resource Availability (Continued)	MacArthur and Levins, 1964, 1967			
Genetic Variation	Grant, 1968 MacArthur, 1965 Shugart and Blaylock, 1973 Van Valen, 1965 Van Valen and Grant, 1970 but see: Soulé, 1970 Soulé and Stewart, 1970 Willson, 1969			
Seasonality		(see Table 5)		
Temporal Predictability		(see Table 5)		
Resource Breadth			Baker, 1971 Grant, 1966 MacArthur and Levins, 1964, 1971 Pianka, 1969 Ricklefs and Cox, 1972 Williams, 1969	



Table 7. Continued

	Resource Breadth	Constancy of Resources	Competition	Resource Availability
Number of Taxa			(see Table 5)	
Precipitation				(see Table 5)
Latitude				(see Table 5)
Stability of Productivity				(see Table 5)
Productivity				(see Table 5)

Resource Breadth is apparently narrowed by increased Resource Availability and limited by sufficient Precipitation, Latitude (determining length of growing season), Stability of Productivity, and amount of Productivity.

Finally, Resource Breadth appears to correlate with Genetic Variation, though this correlation is disputed.

Evenness of Trophic Levels -- The free-body model for Evenness of Trophic Levels (Figure 12) is also relatively simple. Although it consists of five hierarchic levels, it contains a total of only eleven parameters, but with three feed-back loops. References are listed in Table 8.

Evenness of Trophic Levels will be reduced where Seasonality is more marked, because different trophic levels (herbivore, detritivore) will reach peak abundances and diversities at different seasons. Where intensity of Predation is highest, Trophic Level Evenness will also be highest, at least in terrestrial systems where the Eltonian pyramid of numbers or biomass is rarely inverted, because Predation will reduce Competition at the lower trophic levels. If intensity of predation is decreased, Competition will reduce diversity at lower trophic levels and the degree of Evenness of Trophic Levels is restored and Predation may become relatively higher. These interactions thus form a negative feed-back loop. Predation can be made more intense by addition of Trophic Levels, if predators don't completely distinguish the trophic level of their prey, or addition of Trophic Levels can release a lower trophic level from control (compare Hurlbert, Mulla and Willson, 1972, with Hurlbert, Zedler and Fairbanks, 1972). Number of Trophic Levels appears limited by Resource Availability. Influences on Resource Availability are discussed under Number of Taxa. Competition within a trophic level



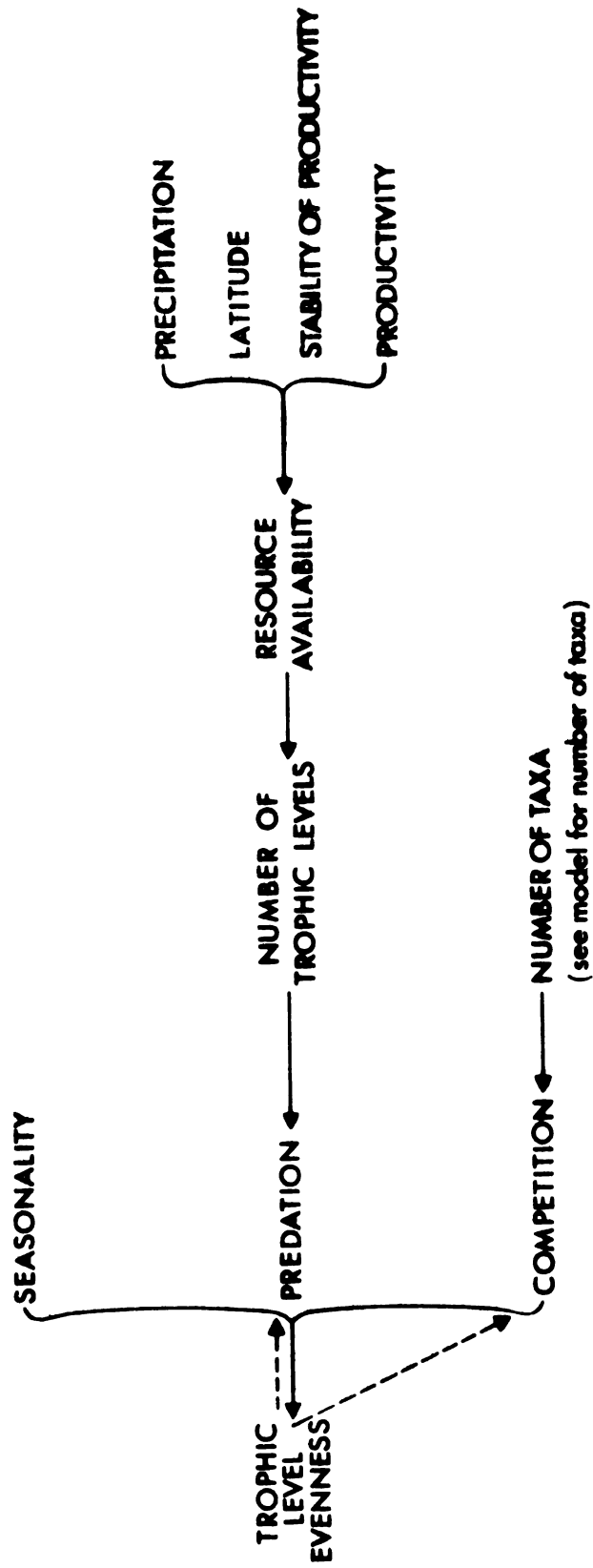


Figure 12. Free-Body Model of Trophic Level Evenness.

Table 8. Table of References Relating Ecological Parameters that Lead to Free-Body Model of Evenness of Trophic Levels.

	Trophic Level Evenness	Predation	Competition	Number of Trophic Levels	Resource Availability
Seasonality	Cameron, 1972				
Predation	Garfinkel and Sack, 1964 Hurlbert, Mulla and Willson, 1972 Hurlbert, Zedler and Fairbanks, 1972 Janzen, 1970 Paine, 1966 Parrish and Saila, 1970 Porter, 1972a	Hurlbert, Mulla and Willson, 1972 Hurlbert, Zedler and Fairbanks, 1972	Garfinkel and Sack, 1964 Hurlbert, Mulla and Willson, 1972 Hurlbert, Zedler and Fairbanks, 1972 Janzen, 1970 Paine, 1966 Parrish and Saila, 1970 Porter, 1972a		
Competition	Paine, 1966 Porter, 1972a				
Number of Trophic Levels		Hurlbert, Mulla and Willson, 1972 Hurlbert, Zedler and Fairbanks, 1972			

Table 8. Continued

Trophic Level	Trophic Level Evenness	Predation	Competition	Number of Trophic Levels	Resource Availability
		Paine, 1966 Porter, 1972a	Hurlbert, Mulla and Willson, 1972 Hurlbert, Zedler and Fairbanks, 1972 Paine, 1966 Porter, 1972a		
Number of Taxa			(see Table 5)		
Resource Availability				Garfinkel and Sack, 1964 Heatwole and Levins, 1972, 1973 Paine, 1966 Simberloff, 1969b Simberloff and Wilson, 1969 Wilson, 1969 Wilson and Simberloff, 1969	
Precipitation					(see Table 6)
Latitude					(see Table 6)

Table 8. Continued

	Trophic Level Evenness	Predation	Competition	Number of Trophic Levels	Resource Availability
Stability of Productivity					(see Table 6)
Productivity					(see Table 6)

can reduce the Number of Taxa in that level and thus alter Trophic Level Evenness, increasing it if lower trophic levels are affected and decreasing it if higher levels are affected. Since Evenness of Trophic Levels can affect relative Predation intensity, and Predation can reduce Competition, we have another feedback loop. Number of Taxa and other parameters influencing Predation are discussed under Number of Taxa.

Trophic Level Distinctness -- The free-body model for Distinctness of Trophic Levels (Figure 13) is highly simplified relative to the other four models. It consists of three hierarchic levels but contains a total of only four parameters and no apparent feed-back loops. The simplicity of this model is almost certainly due to the paucity of published reports that can be in any way associated with Trophic Level Distinctness. Though the distinctness, and indeed the reality, of trophic levels is often debated (e.g., Darnell, 1961), it has never been clearly analyzed. It seems reasonable and also of interest to retain the concept of trophic levels while acknowledging that they may be more distinct in some communities than in others and even developing a means of measuring the degree of their distinctness. References are listed in Table 9.

In an estuarine system which depends largely on production coming unpredictably from outside the system, Trophic Levels appear very indistinct and most organisms feed opportunistically. Where food is unpredictable and variable, communities may not be trophically specialized and structured. These studies suggest that Distinctness of Trophic Levels should be decreased by a decrease in Constancy of Resources. And simulation studies show a two species model to be more stable with just competition or predation interactions between the two species, and not both kinds of interactions.





Figure 13. Free-Body Model of Trophic Level Distinctness.

Table 9. Table of References Relating Ecological Parameters that Lead to Free-Body Model of Distinctness of Trophic Levels.

	Trophic Level Distinctness	Constancy of Resources
Constancy of Resources	Darnell, 1961 Levinton, 1972 Hubbell, 1973a,b	
Seasonality		(see Table 5)
Temporal Predictability		(see Table 5)

System Model and Predictions -- In the system model of expected relationships among the five parameters studied (Figure 14), these five parameters of the system are encircled, while environmental parameters, considered external to this system, are not encircled. Heavy solid arrows between system parameters indicate direct causal effect, while light solid arrows indicate indirect causal effect, mediated by one of the environmental parameters. Dashed and dotted lines between system parameters indicate that those two parameters are both correlated with the same environmental parameter, but may or may not be causally related to each other. Dashed lines indicate either (1) a causal relationship between two environmental parameters, or (2) mediation of an indirect causal relationship between two system parameters by one of the environmental parameters. This mediation arises when two system parameters both have a reciprocal causal relationship with the same environmental parameter, and therefore can affect each other indirectly.

In developing this system model, relationships between any two system parameters which depend on several levels of intermediate parameters as causal links have been excluded. The larger is the number of these intermediate parameters, each related to its own set of parameters, then the smaller is the probability that change in one of the two system parameters being linked will be necessary or sufficient for change in the other of the two. Causation and even correlation will be lost.

Two of the environmental parameters of this model, Resource Availability and Constancy of Resources, are assumed constant in this study. Those parameters which influence these two environmental parameters (see free-body model of Resource Breadth) appear constant. When these two environmental parameters are constant, then the relationships they mediate

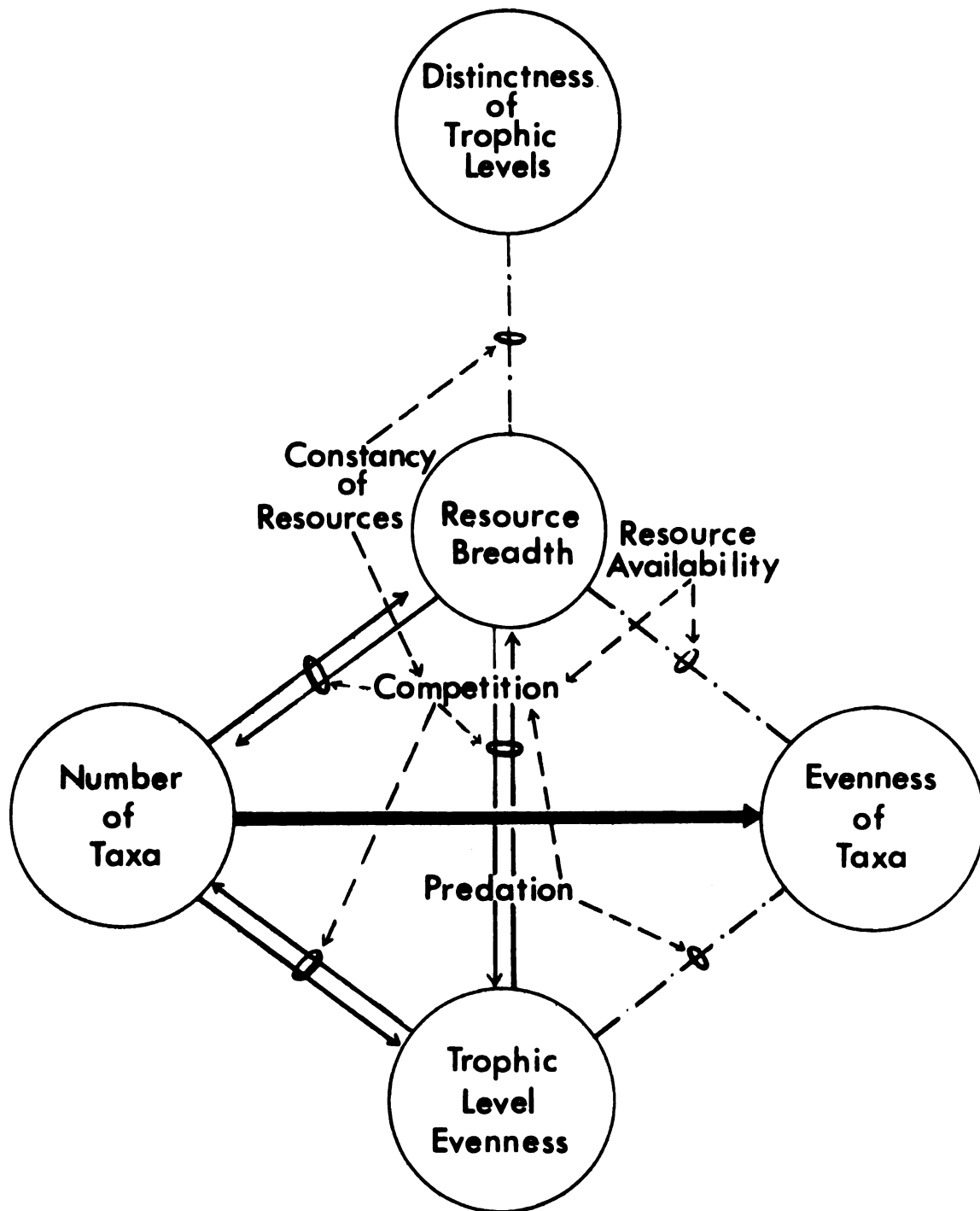


Figure 14. System Model of Interrelationships among the Five Parameters.

will not be detected from the data collected. These relationships are relationships of correlation between (1) Number of Taxa and Resource Breadth, and (2) Resource Breadth and Distinctness of Trophic Levels.

This system model is a complex hypothesis of relationships at the level of community function. It can be tested by drawing predictions from it and then obtaining information which can evaluate the validity of these predictions. If the predictions are not upheld, the system model must be altered and the new model tested. If the predictions are upheld, the model must be further tested perhaps in a more refined way.

Predictions can be made from this system model regarding correlated variation of all ten possible pairs of the five system parameters. These predictions are listed in Table 10. The validity of these predictions is evaluated by applying partial correlation analyses to the data collected in this study.

No correlation is predicted between five parameters pairs. Of these five parameter pairs, four include Distinctness of Trophic Levels as one member of the pair. The free-body model for Distinctness of Trophic Levels is the most simplistic, is derived from the fewest references, and contains the least information. Consequently, confidence in these four predictions is the least.

Table 10. Correlations Between Parameter Pairs Predicted from the System Model.

PARAMETER PAIR	CORRELATION PREDICTED FROM SYSTEM MODEL
NUMBER OF TAXA versus EVENNESS OF TAXA	NEGATIVE
NUMBER OF TAXA versus RESOURCE BREADTH	NEGATIVE
NUMBER OF TAXA versus TROPHIC LEVEL EVENNESS	POSITIVE
NUMBER OF TAXA versus TROPHIC LEVEL DISTINCTNESS	NONE
EVENNESS OF TAXA versus RESOURCE BREADTH	NONE
EVENNESS OF TAXA versus TROPHIC LEVEL EVENNESS	POSITIVE
EVENNESS OF TAXA versus TROPHIC LEVEL DISTINCTNESS	NONE
RESOURCE BREADTH versus TROPHIC LEVEL EVENNESS	POSITIVE
RESOURCE BREADTH versus TROPHIC LEVEL DISTINCTNESS	NONE
TROPHIC LEVEL EVENNESS versus TROPHIC LEVEL DISTINCTNESS	NONE

## ANALYSES

### Estimation of Parameters

The five ecological parameters investigated in this study are estimated indirectly by measuring fourteen variables. Table 11 lists the five parameters and the variables used to estimate them.

In addition, sampling in each community is done at two scales, fine and coarse, and values for each variable are obtained twice. For the fine scale of sampling, values for the variables are obtained for each of the fifteen plots per transect, yielding a total sample size of seventy-five per community, with five transects per community. For a coarse scale of sampling, data within each transect are combined irrespective of plot, and a value for each variable is obtained for each transect, yielding a sample size of five for each community. These five parameters and fourteen variables are discussed in the following subsections. For each discussion please refer to Table 11.

Number of Taxa -- Number of Taxa (N) is estimated by two variables.

Number of Families (NF) is the number of families and orders of invertebrate animals, while Number of Species (NS) is the number of plant species. These variables are measured simply as counts of the Number of Taxa encountered in a plot or in a transect. Since plants are identified to species, but invertebrate animals only to family or order, the NS variable may be expected to provide greater resolution for detecting pattern in variation than the NF variable. Number of species apparently is conservatively estimated by numbers of higher taxa (Simberloff, 1969a). For example, if two communities differ in number of families, they would also differ in number of species, although the reverse would not necessarily be true. It is assumed here that the number of animal

Table 11. Table of Symbols Used to Abbreviate the Five Parameters and the Fourteen Variables Used to Estimate the Parameters.

Parameter	Variable	Name of Parameter or Description of Variable
N		Number of Taxa
	NF	Number of Families or orders of invertebrate animals.
	NS	Number of Species of plants.
E		Evenness of Taxa
	EF	Evenness of Families of invertebrate animals.
	ES	Evenness of Species of plants.
B		Resource Breadth
	BF1	per-cent of animal taxa with a rank of one.
	BF3	per-cent of animal taxa with a rank of three.
	BI1	per-cent of individual animal specimens of rank one.
	BI3	per-cent of individual animal specimens of rank three.
T		Evenness of Trophic Levels
	TF	Evenness by taxa, plants-animals, 4 trophic levels.
	TI	Evenness by individuals, animals only, 3 levels.
D		Distinctness of Trophic Levels
	DF1	per-cent of animal taxa with a rank of one.
	DF3	per-cent of animal taxa with a rank of three.
	DI1	per-cent of individual animal specimens of rank one.
	DI3	per-cent of individual animal specimens of rank three.



families is a conservative estimate of number of animal species, and that any insular or seasonal differences in number of animal families, or correlation of it with other variables, will indicate similar patterns of differences or correlation for number of animal species.

Evenness of Taxa -- Evenness of Taxa (E), like Number of Taxa, is estimated by two variables. Evenness of Families (EF) is the evenness of the distributions of individuals among the invertebrate animal families or orders. Evenness of Species (ES) is the evenness of the distributions of plants among the plant species. Again, plants are identified to species, invertebrate animals to family or order. And again, evenness of distributions of individuals among families is assumed here to be a conservative estimate of the evenness of distributions of individuals among species. It is assumed again that patterns of differences or of correlation, if found, would also hold for species data, perhaps with better resolution.

Evenness is computed according to Hill (1973) by using the Shannon-Wiener information formula (Shannon and Weaver, 1949; Pielou, 1969). The Shannon-Wiener formula calculates an index,  $H'$ , of the information (or diversity) contained in any system of  $N$  cases organized into  $K$  categories, with  $n_i$  cases in category  $k_i$ :

$$H' = - \sum_{i=1}^k \frac{n_i}{N} \ln \frac{n_i}{N}$$

This index  $H'$  is increased either by increasing the number of categories,  $k$ , or by making the number of cases,  $n$ , more nearly equal among the  $k$  categories. The index is a logarithmic function, and exponentiation of  $H'$  yields a number of the  $k$  categories adjusted to that number which would yield the same  $H'$  if the number of cases in each category were

equal, given the same total number of cases, N. Therefore, a sufficient measure of the evenness of the distribution of the N cases among the k categories is the ratio,  $E = \frac{\exp \sqrt{H^*}}{k}$ . When the N cases are distributed equally among the k categories,  $E = 1$ . As the N cases become increasingly unevenly distributed among the k categories, E approaches zero. In the case of Evenness of Taxa in this study, the k categories are either species of plants or families of animals found in a transect or plot, and the N cases are the individual organisms in that transect or plot, so that  $E = \frac{\exp H^*}{(NF \text{ or } NS)}$ .

Resource Breadth -- Resource Breadth (B) pertains only to animals and is estimated by four variables: Resource Breadth by families (BF1, BF3) and Resource Breadth by individuals (BI1, BI3). On the basis of published natural history reports (Arnett, 1960; Blatchley, 1920, 1926; Borror and DeLong, 1971; Bristowe, 1941, 1958; Burch, 1962; Cloudsley-Thompson, 1939; Crowson, 1967; Curran, 1965; Ellis, 1969; Fitch, 1963; Gertsch, 1949; Graham, 1955; Kaston, 1972; Leonard, 1959; Oldroyd, 1964; Purchon, 1968; Stephenson, 1930; Van Name, 1936), the taxa of animals found in this study were each given a rank value of Resource Breadth of either one, two, or three. Animal taxa with very broad feeding habits, i.e., with greatest Resource Breadth, were assigned a rank of three, while those with very narrow feeding habits were assigned a rank of one, and those with intermediate feeding habits were assigned a rank of two. In the case of insects with complete metamorphosis, assignment of these ranks was based on the food habits of the larvae, except in a few cases, such as ants (Formicidae) and fleas (Leptopsyllidae). In both these cases, larval food is often first processed by the adults. In some cases, larvae and

adults feed quite differently, and in most of these cases the adults either do not feed or become nectar feeders. Ground beetles (Carabidae) are an exception to this latter rule, and assignment of ranks was based on adult feeding habits. As examples of how the ranks were assigned, long-horned grasshoppers of the family Tettigoniidae, feed on a wide variety of resources and are correspondingly given a rank of three (see Table 2). Conversely, leafhoppers, of the family Cicadellidae, feed on specific plants and mostly on their leaves, and are given a rank of one (see Table 2). Spiders of the family Lynphiidae have a sensitive palate, will reject some kinds of prey (Bristow, 1958) and feed chiefly on leafhoppers (Fitch, 1963) and are given a rank of two (see Table 2).

Certain assumptions must be made in order to assign rank values of Resource Breadth to families, rather than species, of invertebrates. If it is assumed that in the present study the most common species per family were collected, and that published food habits information was also collected on the most common species, then error in assigning ranks pertains mostly to rare species and contributes a small percentage to the total variation in the data. If these assumptions are valid, error will be increased, resolution will be lost, but any results found will not be reversed. Also, many doubtful cases were either identified to lower taxa or it was ascertained that they were not of lower taxa aberrant for the family in food habits. For example specimens of Tettigoniidae were ascertained not to be members of the sub-family Decticinae, which contains carnivorous species with narrower Resource Breadth than the family in general. Finally, most of the food habits information has been reported in the literature at the family level rather than the species level.

For each plot or transect, the percentage of animals with a rank of one, of two, and of three were computed. The first and third of these three percentages are maintained as variables in this study. These three percentages are not mutually independent, and it is felt that a single index of the three would lose useful information. It is also felt that the two extreme ranks of Resource Breadth would provide the greatest resolution for statistical analyses.

The variables BF1 and BF3 are the percentages of taxa (families) of invertebrate animals, found in a plot or a transect, that were given a rank of one and three, respectively, of Resource Breadth. On the other hand, BI1 and BI3 are the percentages of individual invertebrate animals, in a plot or a transect, given respectively a rank of one and three. The "taxa" variables (BF1 and BF3) will not necessarily vary in the same manner as the "individuals" variables (BI1 and BI3), especially if the more common taxa are more often given a rank of three and rare taxa, a rank of one. (Maguire, 1967, suggests just such differences in abundances of protozoa with different niche sizes.) If these two kinds of variables do clearly behave differently, then we can conclude that common taxa and rare taxa tend to exhibit different degrees of Resource Breadth.

Evenness of Trophic Levels -- Trophic Level Evenness (T) is estimated by two variables. Trophic Level Evenness (TF) is the evenness of plant and animal taxa among four trophic levels. Trophic Level Evenness by individuals (TI) is the evenness of individual animals among three trophic levels. Plant data are frequency data, not counts of individuals, and therefore are not included in calculation of TI.

All organisms recorded in this study are assigned to one of four trophic levels. All plants are, of course, assigned to the producer

trophic level. Each animal taxon is assigned to a herbivore, detritivore, or carnivore trophic level on the basis of published natural history accounts, as for Resource Breadth. Animal taxa which feed on living plant material are assigned to the herbivore trophic level, while those which feed on non-living material are assigned to the detritivore level. Taxa which feed on both living plant material and non-living material are assigned to one of these levels depending on which type of food material makes up the greater proportion of the diet. This information on double function is preserved by giving these taxa a rank of two for Trophic Level Distinctness (see below). As examples, long-horned grasshoppers, family Tettigoniidae, feed mostly on living plant material, though they may feed on dead soft-bodied insects (Borror and DeLong, 1971; Blatchley, 1920) and are classified as herbivores (see Table 2). Conversely, cockroaches, family Blatidae, are rather general feeders, but live chiefly on plant and animal refuse (Borror and DeLong, 1971; Blatchley, 1920) and are classified here as detritivores (see Table 2). All animal taxa which feed on living animal material are assigned to the carnivore trophic level, even those which may also feed on living plant material or non-living material, or both, since their carnivorous feeding is likely to affect more other taxa in the community than their herbivorous or detritivorous feeding. Again, information about taxa which function in more than one trophic level is preserved in Trophic Level Distinctness. The damselfly bugs, Nabidae, are predaceous on many types of insects (Borror and DeLong, 1971), and are classified here as carnivorous. All spiders are also classified as carnivores.

Again, plants are identified to species, animals to family or order. As discussed under Number of Taxa, however, number of animal families may

be expected to conservatively estimate number of animal species. Since information desired in this study pertains to patterns of variation, either insular, seasonal, or in correlation with some other parameter, then it is not necessary to obtain absolute values for Trophic Level Evenness. Use of plant species and animal families in the variable TF provides values that are useful for comparative purposes.

As with Resource Breadth, Evenness of Trophic Levels is estimated by a "taxa" variable (TF) and an "individuals" variable (TI). If organisms at lower trophic levels are more common than carnivores, as might be expected from an Eltonian pyramid of numbers, then these two kinds of variables may behave somewhat differently.

Evenness of Trophic Levels is computed similarly to Evenness of Taxa (above) by the ratio  $E = \exp H'/k$ , where in this case E is either TF or TI,  $H'$  is again the index computed by the Shannon-Wiener formula, and the k categories are the four or three trophic levels. The N cases called for in the Shannon-Wiener formula are either the number of taxa, in TF, or the number of individual organisms, in TI, found in a given plot or transect.

Distinctness of Trophic Levels -- Distinctness of Trophic Levels pertains only to animals and is estimated by four variables: Distinctness of Trophic Levels by families (DF1, DF3) and Distinctness of Trophic Levels by individuals (DI1, DI3). Here as with Resource Breadth, the taxa of animals are each given a rank of one, two or three based on published natural history. Animal taxa which clearly function in a single trophic level (eat only living plant, living animal, or non-living material) are given a rank of three. (They recognize trophic levels most distinctly.) Animals which function in two trophic levels (eat living plant and non-

living material, living animal and non-living material, or living animal and living plant material) are given a rank of two. Taxa which function in all three trophic levels (eat living plant, living animal, and non-living material) are given a rank of one. For example, long-horned grasshoppers, family Tettigoniidae, feed mostly on living plant material, but, as mentioned above under Evenness of Trophic Levels, they will occasionally feed on dead soft-bodied insects. They are therefore given here a rank of two for Distinctness of Trophic Levels (see Table 2). Leafhoppers, of the family Cicadellidae, feed entirely on green plants (Borror and DeLong, 1971) and are given a rank of three for Distinctness of Trophic Levels. Ants, family Formicidae, are given a rank of one, since their foraging often includes living plant material, living animal material, and a wide variety of non-living organic material (see Table 2).

As with Resource Breadth, certain assumptions must be made in order to assign rank values of Distinctness of Trophic Levels to families, rather than species, of invertebrate animals. The same assumptions and arguments presented under Resource Breadth, above, also apply to Distinctness of Trophic Levels in this respect.

As with Resource Breadth, the percentages of animals in a plot or in a transect with a rank of one and those with a rank of three were computed and used as variables in this study. Distinctness of Trophic Levels is also estimated by "taxa" variables (DF1, DF3) and "individuals" variables (DI1, DI3). If these two kinds of variables behave differently, then taxa are differentially common or rare, depending on whether they feed from only one, or two, or even three trophic levels.

Problem Taxa -- For some taxa of animals, natural history information is either confused or lacking. These taxa could not be assigned a rank value of Niche Breadth or Distinctness of Trophic Levels or could not be assigned to a trophic level. These taxa were excluded from the analyses. Taxa thus excluded constituted about two per-cent of all taxa of animals recorded in this study.

#### Analysis of Insular and Seasonal Effects

Insular and seasonal effects on the fourteen variables used to estimate the five parameters (see Table 11) are analyzed by analysis of variance techniques. The data do not meet the assumptions of parametric analysis of variance, and Wilson's non-parametric analysis of variance is used (Wilson, 1956). Each variable is analyzed twice, for the two scales of sampling. Data obtained from fine scale sampling, plots data, are organized into three-way tables for analysis, where columns are the mainland and island communities, or the effect of insularity, and rows are Visits I and II, or the effect of seasonality. Blocks are the five transects per community, and sample size is fifteen plots per cell. Data obtained from coarse scale of sampling, transects data, are organized into two-way tables for analysis, where columns again are mainland and island (insularity), and rows are Visits I and II (seasonality), and sample size is five transects per cell. Data from the two replicates of the study, the Ohio replicate and the Michigan replicate, are analyzed separately.

#### Analysis of Predicted Correlations

Predictions regarding correlation drawn from the system model (see Table 10) are evaluated by partial correlation analysis. In partial



correlation analysis (Kendall and Stuart, 1967; Nie, Bent and Hull, 1970), a correlation coefficient is computed between two variables while other measured variables are statistically controlled.

For both of the two scales of sampling, the fourteen variables used to estimate the five parameters (see Table 11) are divided into two sets of nine variables each, one set for "taxa" variables and one for "individuals" variables. Variables NF and NS, used to estimate Number of Taxa, and variables EF and ES, used to estimate Evenness of Taxa, are not identified as "taxa" or "individuals" variables, and are included in both sets. The "taxa" set of variables thus includes NF, NS, EF, ES, BF1, BF3, TF, DF1 and DF3, while the "individuals" set of variables includes NF, NS, EF, ES, BI1, BI3, TI, DI1 and DI3. Partial correlation coefficients of order seven are computed between all possible pairs of the nine variables within each set. For each coefficient all variables are controlled other than the two contributing the coefficient.

For every pair of variables within each of these two sets, for both replicates of the study (Ohio, Michigan), a total of six partial correlation coefficients are computed. Two of these are general coefficients, computed from all data combined, within a state, from both the mainland and the island communities and from both Visits I and II. One of these general coefficients is computed from plots data, the fine scale of sampling, the other from transects data, the coarse scale of sampling. The remaining four coefficients are all computed from plots data, one from the data of each of the two visits to each of the two communities within a state. Coefficients are not computed from transects data of each visit to each community because the sample size (only five

observations per sample) is too small to permit significance testing of seventh order coefficients.

With six correlation coefficients computed between every pair of variables, within each "taxa" set and each "individuals" set of variables, and within each state, correlation between any two variables can be validated statistically, and the chance of accepting spurious individual correlation coefficients can be reduced. A one-tailed or two-tailed t-statistic is used to test the following null hypothesis: the mean correlation of the six coefficients does not differ from a hypothesized "standard," or parametric mean, of zero correlation. The one-tailed test is applied if a correlation of given sign is predicted between the given pair of variables, while the two-tailed test is applied if no correlation is predicted. Each of the six correlation coefficients is given a value of plus one if its sign is positive, minus one if its sign is negative, or zero if it does not differ significantly from zero. These values are transformed to rankit values (Sokal and Rohlf, 1969), and the t-statistic is computed from these. An alpha level of 0.10 is used for rejection of the null hypothesis. Although even the rankit values may not be distributed according to Student's t-distribution, and any six coefficients are not entirely independent of one another, these tests nevertheless provide objective and comparable criteria to help reduce the probability of accepting spurious correlations.

In the case of one-tailed tests, with correlations of given sign predicted, the critical value of the t-statistic is 1.467 at  $\alpha = .10$  and with degrees of freedom = 5 (Rohlf and Sokal, 1969). This critical value is exceeded, and the null hypothesis rejected, when two or more of six correlation coefficients differ from zero with the same sign, and none

differs from zero with the opposite sign (see Table 12). For two-tailed tests, where no correlation is expected between two variables, the critical value of the t-statistic is 2.015 at  $\alpha = .10$  and with degrees of freedom = 5. This critical value is exceeded, and the null rejected, when three or more of six coefficients differ from zero with the same sign, and none differs from zero with the opposite sign (see Table 12).

Table 12. Table of Critical t-Values and Critical Numbers of Coefficients Used to Validate Correlation Between Variables.

	t(critical)	minimum number of coefficients
one-tailed test	1.467	2
two-tailed test	2.015	3

## RESULTS AND DISCUSSION

### Insularity and Seasonality

Insular and seasonal effects on the five system parameters are summarized in Table 13, both those predicted from the literature and those found in the present study. These results are presented in more detailed form for the fourteen variables used to estimate the parameters, tabulated for both states and for both fine and coarse scales of sampling, in Tables 14-17. In each of these four tables, the median value for each variable is listed, the result of significance testing is indicated for each effect, and the direction of any significant effect is shown.

Number of Taxa -- As Table 13 shows, Number of Taxa was lower on islands than on mainlands, as was predicted. Reference to Tables 14-17, however, shows that this effect is almost limited to plants and is only found for one comparison from the animal data: Number of Families of animals is greater on the mainland than the island for plots data in Michigan. Furthermore, in Michigan, transects data for plants do not show a difference between island and mainland, although plots data show the expected difference. The data generally conform to the theory of island biogeography presented by MacArthur and Wilson (1963).

Lack of an insular effect on the Number of Families of invertebrate animals in Ohio may be due to a greater motility of animals than plants, to the stepping stone effect of two interceding islands in Ohio, to the similar isolation of the island and mainland communities as woodlots which are "islands" of a sort themselves, or to any combination of these. Lack of an insular effect on transects data of Number of invertebrate Families in Michigan may reflect the lack of resolution achieved by this coarse

Table 13. Effects of Insularity and Seasonality on the Five System Parameters.

PARAMETER	EXPECTED EFFECT		EFFECT FOUND	
	Insular Effect	Seasonal Effect	Insular Effect	Seasonal Effect
N	$M_n > I_s$	$I < II$	$M_n > I_s$	$I \geq II$
E	$M_n < I_s$	$I > II$	$M_n \leq I_s$	No Difference
B	$M_n < I_s$	?	Variable	Variable
T	?	$I > II$	$M_n > I_s$	$I \geq II$
D	?	?	$M_n > I_s$ Ohio $M_n < I_s$ Mich	$I < II$

Mn: Mainland Community

I: Visit I

Is: Island Community

II: Visit II

Table 14. RESULTS OF ANALYSES OF VARIANCE OF VARIABLES IN OHIO, PLOTS SCALE OF SAMPLING.

VARIABLE	MEDIAN	EFFECT				
		TOTAL	INSULARITY	SEASONALITY	BLOCK	INTERACTION
NF	8.0	$P \leq .001$	N.S.	$P \leq .001$ I > II	N.S.	N.S.
NS	10.0	$P \leq .01$	$P \leq .001$ $M_n > I_s$	N.S.	$P \leq .01$	N.S.
EF	0.637	$P \leq .001$	$P \leq .01$ $M_n > I_s$	$P \leq .001$ I < II	N.S.	N.S.
ES	0.843	N.S.	$P \leq .05$ $M_n < I_s$	N.S.	N.S.	N.S.
BF1	0.111	$P \leq .05$	N.S.	N.S.	N.S.	$P \leq .01$
BF3	0.571	$P \leq .001$	$P \leq .001$ $M_n < I_s$	N.S.	N.S.	$P \leq .05$
BI1	0.026	$P \leq .05$	N.S.	N.S.	N.S.	$P \leq .01$
BI3	0.673	$P \leq .001$	$P \leq .001$ $M_n < I_s$	$P \leq .001$ I > II	N.S.	$P \leq .05$
TF	0.772	$P \leq .001$	N.S.	$P \leq .001$ I > II	N.S.	N.S.
TI	0.833	$P \leq .05$	$P \leq .01$ $M_n > I_s$	N.S.	N.S.	N.S.
DF1	0.167	$P \leq .001$	$P \leq .001$ $M_n < I_s$	N.S.	N.S.	N.S.
DF3	0.750	$P \leq .001$	$P \leq .001$ $M_n > I_s$	N.S.	N.S.	N.S.
DI1	0.087	$P \leq .001$	$P \leq .001$ $M_n < I_s$	N.S.	N.S.	$P \leq .001$
DI3	0.857	$P \leq .001$	$P \leq .001$ $M_n > I_s$	N.S.	N.S.	$P \leq .05$

Table 15. RESULTS OF ANALYSES OF VARIANCE OF VARIABLES IN OHIO, TRANSECTS SCALE OF SAMPLING.

VARIABLE	MEDIAN	EFFECT			
		TOTAL	INSULARITY	SEASONALITY	INTERACTION
NF	30.5	$P \leq .01$	N.S.	$P \leq .001$ I > II	N.S.
NS	36.5	N.S.	$P \leq .01$ $M_n > I_s$	N.S.	N.S.
EF	0.292	N.S.	N.S.	N.S.	N.S.
ES	0.671	N.S.	$P \leq .01$ $M_n < I_s$	N.S.	N.S.
BF1	0.247	N.S.	N.S.	N.S.	N.S.
BF3	0.493	N.S.	N.S.	N.S.	N.S.
BI1	0.033	N.S.	N.S.	N.S.	$P \leq .01$
BI3	0.621	$P \leq .05$	$P \leq .01$ $M_n > I_s$	N.S.	N.S.
TF	0.820	$P \leq .05$	N.S.	$P \leq .01$ I > II	N.S.
TI	0.890	$P \leq .05$	$P \leq .01$ $M_n > I_s$	N.S.	N.S.
DF1	0.092	$P \leq .05$	N.S.	$P \leq .01$ I > II	N.S.
DF3	0.783	N.S.	N.S.	N.S.	N.S.
DI1	0.103	$P \leq .01$	$P \leq .001$ $M_n < I_s$	N.S.	N.S.
DI3	0.838	$P \leq .001$	$P \leq .001$ $M_n > I_s$	N.S.	N.S.



Table 16. RESULTS OF ANALYSES OF VARIANCE OF VARIABLES IN MICHIGAN,  
PLOTS SCALE OF SAMPLING.

VARIABLE	MEDIAN	EFFECT				
		TOTAL	INSULARITY	SEASONALITY	BLOCK	INTERACTION
NF	6.0	$P \leq .001$	$P \leq .001$ $M_n > I_s$	N.S.	$P \leq .01$	$P \leq .05$
NS	13.0	N.S.	$P \leq .05$ $M_n > I_s$	N.S.	N.S.	N.S.
EF	0.856	$P \leq .001$	$P \leq .001$ $M_n < I_s$	N.S.	$P \leq .001$	N.S.
ES	0.835	N.S.	$P \leq .01$ $M_n < I_s$	N.S.	N.S.	N.S.
BF1	0.0	N.S.	N.S.	N.S.	N.S.	N.S.
BF3	0.625	N.S.	N.S.	N.S.	N.S.	N.S.
BI1	0.0	N.S.	N.S.	N.S.	N.S.	N.S.
BI3	0.632	$P \leq .001$	N.S.	$P \leq .001$ $I < II$	N.S.	$P \leq .01$
TF	0.687	N.S.	$P \leq .05$ $M_n > I_s$	N.S.	N.S.	N.S.
TI	0.867	N.S.	N.S.	N.S.	$P \leq .05$	N.S.
DF1	0.0	N.S.	N.S.	N.S.	N.S.	N.S.
DF3	0.833	N.S.	$P \leq .05$ $M_n < I_s$	N.S.	N.S.	N.S.
DI1	0.0	N.S.	N.S.	N.S.	N.S.	N.S.
DI3	0.903	N.S.	N.S.	$P \leq .05$ $I < II$	N.S.	N.S.

Table 17. RESULTS OF ANALYSES OF VARIANCE OF VARIABLES IN MICHIGAN,  
TRANSECTS SCALE OF SAMPLING.

VARIABLE	MEDIAN	EFFECT			
		TOTAL	INSULARITY	SEASONALITY	INTERACTION
NF	28.0	N.S.	N.S.	N.S.	N.S.
NS	36.0	N.S.	N.S.	N.S.	N.S.
EF	0.467	N.S.	N.S.	N.S.	N.S.
ES	0.586	N.S.	N.S.	N.S.	N.S.
Bf1	0.200	$P \leq .05$	N.S.	N.S.	$P \leq .05$
Bf3	0.536	N.S.	N.S.	N.S.	N.S.
B11	0.048	N.S.	N.S.	N.S.	N.S.
B13	0.625	$P \leq .01$	N.S.	$P \leq .001$	N.S.
TF	0.786	N.S.	N.S.	$I < II$ N.S.	N.S.
T1	0.790	$P \leq .05$	$P \leq .01$	N.S.	N.S.
DF1	0.069	N.S.	$M_n > I_s$ N.S.	N.S.	N.S.
DF3	0.792	$P \leq .05$	N.S.	$P \leq .01$	N.S.
D11	0.054	$P \leq .05$	$P \leq .01$	$I < II$ N.S.	N.S.
D13	0.866	N.S.	$M_n > I_s$ N.S.	N.S.	N.S.

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scale of sampling, or may reflect different scales of pattern of diversity in the community. Alternatively, the insular effect found on plots data in Michigan may be accidental or spurious.

Lack of an insular effect on transects data of Number of Plant Species in Michigan suggests either of two possible conclusions, that resolution is lower at the transects scale of sampling or that the coarse scale of sampling represents a different scale of pattern of diversity in the community.

It was predicted that Number of Taxa would increase during the summer season, and, as Table 13 shows, the reverse effect was actually found. Reference to Tables 14-17 shows that this effect occurs only in Number of Families of invertebrate animals in the Ohio replicate of the study. But where found, this effect is very strong, with probability of less than 0.001 of no difference between visits, for both plots and transects data.

A significant block effect and interaction effect for Michigan plots data, Number of Families of invertebrates, reflects an aberrantly low mean value for one of the mainland transects during the second visit.

Evenness of Taxa -- Evenness of Taxa is expected to be lower on mainlands than islands. Table 13 shows that this difference is found. But reference to Tables 14-17 shows some inconsistency. This difference is clearly found for plant data, for both Ohio and Michigan at the plots scale of sampling, and for Ohio at the transects scale of sampling also. No difference was found for Evenness of Species of plants in Michigan for the transects scale of sampling. The animal data is less consistent. Island is found to be greater than mainland, as expected, in Michigan at the plots scale of sampling, but no difference between island and mainland

was found in either state at the transects scale of sampling, and island was actually lower than mainland in Ohio at the plots scale of sampling.

Lack of an insular effect on Evenness of Taxa, for animals in Ohio and for both plants and animals in Michigan, at the transects scale of sampling, again may reflect either lower resolution or a different scale of pattern of diversity at that scale of sampling.

In every comparison where an insular effect was found on Number of Taxa, a reverse effect was found on Evenness of Taxa. The one aberrant comparison, where island Evenness of Taxa was actually lower than that on mainland in Ohio for plots data, is also the only comparison where an insular effect was found on Evenness of Taxa but not on Number of Taxa. It may be hypothesized that reduction of taxa on islands may differentially involve rare or uncommon taxa, increasing Evenness of Taxa on islands.

It was predicted that Evenness of Taxa would decrease during the summer season. However, Table 13 indicates that no differences were found. As Tables 14-17 show, this is true of all data except for Ohio plots data. This one set of data showed Evenness of Families of invertebrate animals to increase during the summer, a direction of change opposite that expected. This one effect may again have been related to changes in weather factors such as precipitation.

Resource Breadth -- Resource Breadth is expected to be greater on islands than on mainlands, but where significant differences are found, they are somewhat inconsistent (Table 13). Tables 14-17 show that indeed, for the plots scale of sampling in Ohio, Resource Breadth of taxa (BF3) and of individuals (BI3) are greater on the island than the mainland. However, still in Ohio, transects data for individuals (BI3) is greater on the mainland, and no other comparisons in Ohio and none in Michigan showed

significant differences. These variables that do show differences (BF3 and BI3, plots, and BI3, transects) all deal with the percentages of animals assigned a rank of three for Resource Breadth, and the rank of three represents greatest Resource Breadth. Thus, the direction of differences in these variables reflects differences in the same direction in Resource Breadth.

Insular and seasonal effects on Resource Breadth vary and may differ between states. However, a reversal of insular effect between transects and plots data in Ohio suggests the possible conclusion that there is some difference between the two scales of sampling other than simply loss of resolution at the transects scale. Alternatively this reverse effect may merely reflect the variable and inconsistent effect of insularity on Resource Breadth. There also exists the possibility that the methods chosen for measuring Resource Breadth are inadequate. Significant insular or seasonal effects found on any of the variables estimating Resource Breadth are largely restricted to "individuals" variables. "Individuals" variables may provide more resolution, as there are more individuals to work with than there are taxa. The alternative conclusion is that insularity and seasonality differentially influence the population sizes of taxa assigned different ranks but do not influence the number of those taxa.

No prediction was made regarding any seasonal effects on Resource Breadth, and as Table 13 indicates, results showed no definite pattern. Reference to Tables 14-17 shows that in Ohio, Resource Breadth, sampled by plots for individuals (BI3), decreased during the summer season, but that there were no other significant Ohio differences. In Michigan, in contrast, Resource Breadth increased during the summer season for

individuals sampled by plots and also for individuals sampled by transect. These variable results suggest that Resource Breadth is not directly influenced by either insularity or seasonality.

However, Ohio data, at both scales of sampling, show several statistically significant interaction effects which generally indicate that the insular effect is reversed during the season. That is, the mainland has lower Resource Breadth than island during Visit I but higher during Visit II. An alternative way of saying the same thing is that the seasonal effect is reversed between mainland and island. That is, that Resource Breadth increases during the summer season on the mainland but decreases on the island.

Michigan plots data show a significant interaction effect for one of the "individuals" variables (BI3) which suggests that the seasonal effect is not exactly consistent across all blocks (transects).

Evenness of Trophic Levels -- No prediction was made regarding any insular effect on Evenness of Trophic Levels. As Table 13 shows, however, in all cases where significant differences were found, Evenness of Trophic Levels was higher on mainlands than on islands. Tables 14-17 indicate these differences. In Ohio, "individuals" variables (TI) were greater on the mainland than on the island at both scales of sampling, while "taxa" variables did not differ between the two communities. In Michigan, Trophic Level Evenness by "individuals" was again greater on the mainland, but only for the transects scale of sampling. Also, Trophic Level Evenness by "taxa" was higher on the mainland in Michigan, but only for plots scale of sampling in this case.

Again, "individuals" data may provide more resolution, or insularity may differentially influence population sizes of taxa but not numbers of

taxa at different trophic levels. An additional difference is that plant data are not included in computation of Evenness of Trophic Levels by individuals. The one comparison where insularity affects Evenness of Trophic Levels by taxa, the plots scale of sampling in Michigan, with an effect opposite to that in other comparisons where an insular effect was found, is also the only comparison where insularity decreases the Number of Families of animals. It may be that, in general by taxa, decrease only in Number of Species of plants counterbalances a decrease in Evenness of Trophic Levels indicated by individuals data on islands. These results suggest a higher proportion of individual predatory animals, but not of predatory animal taxa, on islands. Any reasons why this should be so are obscure.

It was tentatively predicted that Trophic Level Evenness would decrease during the summer season, and as Table 13 shows, this was indeed the direction of difference for those significant differences found. As Tables 14-17 show, Trophic Level Evenness decreases during the summer only in Ohio and only for "taxa" variables (TF), but for both plots and transects scales of sampling. No other comparisons showed significant differences. This decrease during the summer season for taxa data in Ohio probably reflects a similar decrease in Number of Families of animals, also in Ohio, which would form the top of an Eltonian pyramid. This seasonal effect on Number of Families of animals in Ohio is discussed above.

Distinctness of Trophic Levels -- No predictions were made regarding either insular or seasonal effects on Distinctness of Trophic Levels, but as Table 13 shows, effects were found. The effect of insularity was reversed in direction between the two states. In Ohio, Trophic Level



Distinctness was greater on the mainland than the island. Tables 14-17 show that this is true for taxa data at the plots scale of sampling (DF3 greater on the mainland, DF1 lower on the mainland) but that no difference is shown for the transects scale of sampling. It is also true for individuals data (again, DI3 greater on the mainland, DI1 lower on the mainland) at both the plots and the transects scales of sampling. In Michigan, only one comparison shows a significant difference, and it is reversed to that found in Ohio. Individuals data (DI1) is greater on the mainland for the transects scale of sampling. This indicates a larger percentage of animals with small values of Distinctness of Trophic Levels on the mainland, so that the value of Distinctness of Trophic Levels is lower on the mainland.

The two replicates of the study, in Ohio and in Michigan, differ in several ways. The dominant canopy species differ, the Ohio communities are isolated woodlots while the Michigan communities are localities in extensive forests, latitude is lower in Ohio, topography is more regular in Ohio, and two additional islands can serve as stepping stones between the Ohio island community and the mainland. It is also possible that the one Michigan comparison showing an insular effect is spurious and aberrant.

It is possible that immigration rate is highest on the Ohio island, that it therefore has a higher proportion of invading species than the other communities, and that these invading species may recognize less Distinctness of Trophic Levels in feeding. It is also possible that, in the Ohio island community, a less diverse resource base, represented by lower Number of Species of plants, selects for less trophically specialized organisms in the higher trophic levels. These results are not clarified by the variable effect of insularity on Resource Breadth in

Ohio. Increase in predatory animals on islands, suggested by the results of the insular effect on Trophic Level Evenness (see above), may not include such animals as spiders, which clearly distinguish trophic levels. However, Drew (1967) found more individuals spiders on Beaver Island, Michigan, than on the nearby mainland.

Only a few comparisons show a significant seasonal effect on Distinctness of Trophic Levels, but these all show the same effect, that Distinctness of Trophic Levels increases during the summer season (see Table 13). Tables 14-17 show that in Ohio for taxa data at the transects scale of sampling, the percentage of animals assigned a rank of one (DF1) decreases during the summer, indicating that Distinctness of Trophic Levels increases during the summer. In Michigan, for plots data, the percentage of individual animals given a rank of three (DI3) increases during the summer, and for transects data, the percentage of taxa of animals given a rank of three (DF3) also increases during the summer, both indicating such an increase in Distinctness of Trophic Levels during the summer season. This effect may be due to an increase in Number of Taxa of such animals as spiders late in the summer. Pulliam, Odum and Barret (1968) show that the number of spider taxa increases during the summer season in a field of millet more slowly than other arthropod species.

Individuals data at the plots scale of sampling (DI1 and DI3) show statistically significant interaction effects which suggest that the insular effect is not consistent across all blocks (transects).

#### Predicted Correlations

Correlations between pairs of the five system parameters are summarized in Table 18. The ten parameter pairs are listed in the first column and the correlations between them that are predicted from the

Table 18. SUMMARY OF RESULTS OF PARTIAL CORRELATION ANALYSES OF THE FIVE SYSTEM PARAMETERS.

Parameter Pair	Correlation		Comments	Conclusion
	Ex-pected	Found		
N-E 4	-	- 0	Within invertebrate animals. Within plants and between plants and animals.	Prediction partially verified.
N-B 8	-	- 0	Within invertebrate animals. Between plants and animals.	Prediction partially verified.
N-T 4	+	+ - 0	Within invertebrate animals. With plants: taxa variables. With plants: individuals var.	Prediction found invalid.
N-D 8	0	- 0	Within invertebrate animals: individuals variables. Between plants and animals.	Prediction found invalid.
E-B 8	0	0 0	(-) tendency in Ohio. In all cases in Michigan.	Prediction verified.
E-T 4	+	+ 0	Within invertebrate animals: individuals variables. In all other cases.	Prediction partially verified.
E-D 8	0	- 0	Within invertebrate animals. With plants.	Prediction found invalid.
B-T 8	+	0	In all cases.	Prediction found invalid.
B-D 16	0	0	In all cases.	Prediction verified.
T-D 8	0	0 +	In virtually all cases. For a single variant, a taxa variable in Michigan.	Prediction verified.

See text for further explanation of table.

system model in the second column. In the third column correlations found in this study are tabulated, with slightly more detail. The "Comments" column characterizes this detail, and the last column concludes, for each parameter pair, whether the predicted correlation is verified or found invalid. This general conclusion is based on the following criteria. If no correlation is predicted between two parameters, the prediction is found invalid only if a correlation is found between more than one pair of the variables estimating the parameter, and is otherwise verified. If a correlation is predicted between two parameters, the prediction is found invalid only if a correlation of sign opposite that predicted is found between more than one pair of the variables estimating the parameters, or if no correlation is found between all, or all but one, pair of variables, and is otherwise verified or partially verified.

These results are presented in more detail in Table 19. The sign of seventh order partial correlation between the pairs of variables with both the "taxa" set of variables and the "individuals" set of variables is indicated for both the Ohio and the Michigan replicates of the study. For each pair of variables within each set and for each state, the number of coefficients showing a negative correlation, no significant correlation and a positive correlation are recorded under the three columns, (-), (0) and (+), respectively. There are six of these coefficients for each set of variables (see Analyses -- Analysis of Predicted Correlations, above). A companion column to the (-), (0) and (+) columns within each set, labeled "Results", lists the result of the t-test of the sign of the coefficients.

Table 19. Frequency of Correlation Coefficients of Minus, Zero, or Plus Value Between each Variable Pair for each State and Type of Variable, and Results of t-Test Validation.

Parameters	Variable Pairs	Expected Correlation	OHIO		MICHIGAN	
			"Taxa" Variables	"Individuals" Variables	"Taxa" Variables	"Individuals" Variables
N	NS-NP	+	- 0 2 4 +	- 0 5 1 0	- 0 2 4 +	- 0 + Result
N	NF-EF	-	3 3 0 -	5 1 0 -	4 2 0 -	1 5 0 0
	NF-ES	-	0 6 0 0	0 6 0 0	0 6 0 0	0 6 0 0
	NS-EF	-	0 6 0 0	0 5 1 0	1 5 0 0	1 5 0 0
	NS-ES	-	0 6 0 0	0 6 0 0	1 5 0 0	2 4 0 -
N-B	NF-B*1	+	0 5 1 0	0 3 3 +	0 2 4 +	0 3 3 +
	NF-B*3	-	1 5 0 0	2 4 0 -	0 6 0 0	1 4 1 0
	NS-B*1	+	0 4 2 +	0 5 1 0	0 6 0 0	0 6 0 0
	NS-B*3	-	0 6 0 0	0 5 1 0	0 6 0 0	1 5 0 0
N-T	NF-T*	+	0 0 6 +	0 1 5 +	0 0 6 +	1 4 1 0
	NS-T*	+	5 1 0 -	0 6 0 0	6 0 0 -	1 4 1 0
N-D	NF-D*1	0	1 5 0 0	0 6 0 0	0 4 2 0	0 3 3 +
	NF-D*3	0	0 6 0 0	4 2 0 -	1 5 0 0	2 4 0 0
	NS-D*1	0	1 5 0 0	0 6 0 0	0 6 0 0	0 6 0 0
	NS-D*3	0	2 3 1 0	0 6 0 0	0 5 1 0	0 6 0 0
E	EF-ES	+	1 5 0 0	0 6 0 0	0 6 0 0	0 6 0 0
E-B	EF-B*1	0	0 6 0 0	0 6 0 0	0 6 0 0	0 4 2 0
	EF-B*3	0	2 4 0 0	3 3 0 -	0 6 0 0	1 4 1 0
	ES-B*1	0	0 6 0 0	0 6 0 0	0 6 0 0	0 6 0 0
	ES-B*3	0	0 6 0 0	0 5 1 0	0 6 0 0	0 6 0 0
E-T	EF-T*	+	0 6 0 0	0 1 5 +	0 6 0 0	0 2 4 +
	ES-T*	+	0 6 0 0	0 6 0 0	0 6 0 0	0 5 1 0
E-D	EF-D*1	0	0 6 0 0	0 5 1 0	0 6 0 0	0 6 0 0
	EF-D*3	0	1 5 0 0	3 3 0 -	3 3 0 -	5 1 0 -
	ES-D*1	0	0 6 0 0	0 6 0 0	0 6 0 0	0 6 0 0
	ES-D*3	0	0 6 0 0	0 6 0 0	0 6 0 0	0 6 0 0
B	B*1-B*3	-	6 0 0 -	2 4 0 -	5 1 0 -	4 2 0 -
E-T	B*1-T*	+	0 4 2 +	0 6 0 0	1 5 0 0	0 6 0 0
	B*3-T*	-	1 5 0 0	2 4 0 -	0 6 0 0	1 5 0 0

Table 19. Continued

Parameters	Variable Pairs	Expected Correlation	OHIO						MICHIGAN					
			"Taxa" Variables			"Individuals" Variables			"Taxa" Variables			"Individuals" Variables		
			-	0	+	Result	-	0	+	Result	-	0	+	Result
B-D	B*1-D*1	0	0	6	0	0	0	6	0	0	0	6	0	0
	B*1-D*3	0	0	6	0	0	0	6	0	0	0	6	0	0
	B*3-D*1	0	0	4	2	0	0	5	1	0	0	5	1	0
	B*3-D*3	0	2	4	0	0	2	4	0	0	1	5	0	0
D	D*1-D*3	-	5	1	0	-	6	0	0	-	5	1	0	-
D-T	D*1-T*	0	1	5	0	0	0	6	0	0	0	6	0	0
	D*3-T*	0	2	3	1	0	1	5	0	0	0	3	3	+

\* Indicates the letter "F" for "Taxa" Variables or the letter "I" for "Individuals" Variables. See text for further explanation of table.

It must be remembered that any variable correlating with one of the variables involving the percentages of animals assigned a rank of one for Resource Breadth or Distinctness of Trophic Levels, BF1, BI1, DF1, DI1, is actually showing the reverse correlation with the parameter itself, since a rank of one indicates low values for either parameter. Correlation with a variable involving assignment of rank three (BF3, BI3, DF3, DI3), however, indicates correlation in the same direction with the parameter itself, because a rank of three indicates high value for both parameters.

Any correlations found, those supporting predictions as well as those refuting hypotheses, may represent direct causation, may arise from common correlation with a third parameter, or may be spurious. Spurious correlations are hopefully eliminated by the statistical t-test criteria used above to validate correlations between pairs of variables. Direct causation cannot be investigated in this study. Although many possible sources of common correlation cannot be investigated here, two of the more likely sources can be evaluated by comparing the results of analyses of insular and seasonal effects on the five system parameters with the results of partial correlation analyses of relationships among them.

Number of Taxa versus Evenness of Taxa -- A negative correlation is predicted between Number of Taxa and Evenness of Taxa and is only found (Table 18) between Number of Families of invertebrate animals (NF) and Evenness of Families of invertebrate animals (EF) for both states (Table 19). No significant correlation is found between Evenness and Number of Taxa either within plants or between plants and animals. The prediction in this case is partially verified.

Analyses of variance results indicate that where Number of Families of invertebrates is greater on mainlands, Evenness of Families of

invertebrates is consistently smaller on mainlands. Factors of seasonality appear to have limited inverse effect on these two parameters. The most parsimonious explanation of the negative correlation found between Number of Taxa and Evenness of Taxa apparently is that they are correlated in common, although in inverse manner, with factors of insularity. Reports in the literature provide evidence of a relationship between Number of Taxa and Evenness of Taxa, and provide speculation at most of the causality and mechanisms of that relationship. It is possible, and parsimonious, that this reported relationship arises from common correlation of the two parameters with factors of insularity or other factors.

Number of Taxa versus Resource Breadth -- A negative correlation is also predicted between Number of Taxa and Resource Breadth and again is found (Table 18) between Number of Families of animals (NF) and individuals variables of Resource Breadth (BI1, BI3), in Ohio (Table 19). No significant correlation is found between Number of Species of plants (NS) and Resource Breadth by any variable. The prediction in this case is partially verified.

Results of analyses of variance indicate that factors of insularity and also factors of seasonality have effects on Number of Taxa and Resource Breadth (BF1, BF3, BI1, BI3), but these effects do not show a relationship between the two parameters. These results suggest that animal taxa readily gained or lost from a community, that is, with the least stable population dynamics, are also the animals with the least Resource Breadth, that is, the most specialized feeding behavior. This suggestion is contrary to the theories of fugitive species (Hutchinson, 1959) and of opportunistic species undergoing "r-selection" (MacArthur and Wilson, 1967).



Number of Taxa versus Evenness of Trophic Levels -- A positive correlation is predicted between Number of Taxa and Evenness of Trophic Levels and is found between Number of Families of animals (NF) and Evenness of Trophic Levels (Table 18) for taxa variables (TF) in both states and for individuals variables (TI) in Ohio but not in Michigan (Table 19). However, a negative correlation is found between Number of Species of plants and taxa variables of Evenness of Trophic Levels (TF) in both states. No significant correlation occurs between Number of Species of plants and individuals variables (TI). In a terrestrial system, as in the present study, where an Eltonian pyramid is not likely to be reversed, an increase in the number of taxa of plants would widen the base of the pyramid and hence decrease the Evenness of Trophic Levels. An increase in the number of animal taxa, however, especially higher level consumers, would widen the apex of the pyramid and increase the Evenness of Trophic Levels. The correlations found here either reflect these considerations, or the assumption is invalid that animal families conservatively estimate animal species. The prediction in this case is refuted but apparently clarified.

Results of analyses of variance indicate that either the factors of insularity or the factors of seasonality have effects in a similar direction for all variables affected, both for Number of Taxa and Evenness of Trophic Levels. These results are inconsistent with the opposing correlations of animal taxa and plant taxa with Evenness of Trophic Levels, and it must be concluded that these two parameters are not commonly correlated either with factors of insularity or with factors of seasonality.

Number of Taxa versus Distinctness of Trophic Levels -- No correlation is predicted between Number of Taxa and Distinctness of Trophic Levels.

However, a negative correlation is found (Table 18) between Number of Families of animals (NF) and individuals variables of Distinctness of Trophic Levels (DI1, DI3) (Table 19). No significant correlations were found between any of the other pairs of variables for this pair of parameters. The prediction of no relationship in this case is found invalid.

Results of analyses of variance suggest that Number of animal Taxa is greater on mainlands than on islands in Michigan, while estimates of Distinctness of Trophic Levels are lower on the mainland. These results suggest a negative correlation between the two parameters, and a parsimonious conclusion is that Number of Taxa and Distinctness of Trophic Levels are commonly correlated with factors of insularity. Ohio analyses of variance provide no information to affect this conclusion. There is little or no apparent affect by the factors of seasonality on any of these variables in the analyses of variance and hence common correlation with these factors does not appear to influence the correlation between Number of Taxa and Distinctness of Trophic Levels. The simplest free-body model is that for Distinctness of Trophic Levels, primarily because it is derived from the fewest sources. It is therefore probably the most incomplete, and the conclusion of common correlation of Number of Taxa and Distinctness of Trophic Levels with factors of insularity must be considered tentative until more is known of the parameter Distinctness of Trophic Levels.

Evenness of Taxa versus Resource Breadth -- No correlation is predicted between Evenness of Taxa and Resource Breadth, and in fact no significant

correlation is found (Table 18), except between a single pair of parameters. A negative correlation shows up between Evenness of Families of animals (EF) and Resource Breadth by individuals (BI3) in Ohio (Table 19). Analyses of variance indicate that in this comparison these two parameters may both be influenced by factors of insularity in Ohio. Seasonality appears to have no influence on this result. It is concluded that the prediction of no relationship between Evenness of Taxa and Resource Breadth is verified.

Evenness of Taxa versus Evenness of Trophic Levels -- A positive correlation is predicted between Evenness of Taxa and Evenness of Trophic Levels and is in fact found (Table 18) between Evenness of Families of animals (EF) and Evenness of Trophic Levels by individuals (TI) in both states (Table 19). Other pairs of variables for these two parameters are not significantly correlated. The prediction in this case is partially verified.

Analyses of variance indicate that Evenness of Families of animals (EF) and Evenness of Trophic Levels by individuals (TI) are apparently not commonly correlated with factors of insularity. Seasonality appears to have slight and inconsistent effect on these two parameters. Information in this report appears insufficient at this time to generate any hypotheses to explain the positive correlation found between these two parameters.

Evenness of Taxa and Distinctness of Trophic Levels -- Lack of any correlation is predicted between Evenness of Taxa and Distinctness of Trophic Levels. However, a negative correlation appears (Table 18) between Evenness of Families of animals (EF) and Distinctness of Trophic Levels by individuals (DI1, DI3) but not by taxa in Ohio and by both

individuals and taxa (DI1, DI3, DF1, DF3) in Michigan (Table 19).

Evenness of Species of plants shows no correlation with Distinctness of Trophic Levels. The prediction in this case is found to be invalid.

Results of analyses of variance show that the variables used to estimate Evenness of Taxa and those used to estimate Distinctness of Trophic Levels generally are greater on mainland than on island in Ohio and smaller on mainland than island in Michigan. These results would suggest a positive correlation between Evenness of Taxa and Distinctness of Trophic Levels in Ohio, but a negative correlation is found between them. Hence, this correlation has some other origin than common correlation with factors of insularity. Since both these parameters appear to be related to Number of Taxa by common correlation with factors of insularity, at least two factors must constitute insularity. There is little or no apparent effect by seasonality on any of these variables and hence common correlation with these factors does not appear to influence this correlation. These results suggest a relationship between taxa of animals that do not clearly distinguish the trophic levels from which they feed and taxa that tend to be either rare or dominant or both.

Resource Breadth versus Evenness of Taxa -- A positive correlation is predicted between Resource Breadth and Evenness of Trophic Levels.

However, no significant correlation is found between any of the pairs of variables for these two parameters (Table 18, Table 19). The prediction in this case is found to be invalid. Results of analyses of variance provide no explanation for the lack of validity of this prediction.

It may be conjectured that an inverse causal relationship exists between Number of Taxa and Resource Breadth and also between Number of Taxa and Evenness of Trophic Levels, and that these relationships



counteract any relationship between Resource Breadth and Evenness of Trophic Levels. From the information in this study, no other hypothesis can at present be formulated to explain the absence of the predicted negative correlation between Resource Breadth and Evenness of Trophic Levels.

Resource Breadth versus Distinctness of Trophic Levels -- No correlation is predicted between Resource Breadth and Distinctness of Trophic Levels, and indeed no significant correlation is found (Table 18) between any pair of variables for these two parameters (Table 19). The prediction in this case is verified.

Evenness of Trophic Levels versus Distinctness of Trophic Levels -- Lack of any correlation is predicted between Evenness of Trophic Levels and Distinctness of Trophic Levels, and no correlation is indeed found (Table 18) between all but a single pair of variables for these two parameters. As a single exception, Evenness of Trophic Levels by taxa (TF) shows a positive correlation with Distinctness of Trophic Levels by taxa (DF3) in Michigan only (Table 19). The prediction in this case is verified.

### Predicted Correlations

The system model developed from review of literature leads to ten predictions regarding correlation between pairs of parameters. Six of these predictions are either verified or partly verified, and have failed to be falsified. Four other predictions are found to be invalid. Two of these, however, involve Distinctness of Trophic Levels as one of the pair of parameters, and the confidence of the predictions was not high. In the case of a third prediction, falsification apparently clarified, rather than rejected, the relationship predicted. It must be concluded

that the general structure of this model is valid, though modification of certain relationships within it is required, leading to a revised system model (Figure 15).

The hypothesized relationship between Number of Taxa and Evenness of Taxa is changed to one of common correlation with factors of insularity. (See Figures 14 and 15). The relationship between Number of Taxa and Resource Breadth is upheld. The relationship between Number of Taxa and Evenness of Trophic Levels is clarified by breakdown of Number of Taxa into number of animal families and number of plant species. A relationship is discovered between Number of Taxa and Distinctness of Trophic Levels; its source may or may not be common correlation with factors of insularity. The lack of relationship between Evenness of Taxa and Evenness of Trophic Levels is only partially upheld, possibly indicating that other related parameters may complicate this relationship. A relationship of unknown source is discovered between Evenness of Taxa and Distinctness of Trophic Levels. The relationship between Resource Breadth and Evenness of Trophic Levels is lost for unknown reasons. Relationships between Evenness of Taxa and Resource Breadth, Resource Breadth and Distinctness of Trophic Levels, and Distinctness of Trophic Levels and Evenness of Trophic Levels are all zero as expected, and no new information about them is provided.

Now that the general structure of these models has withstood experimental test, and there is reasonable confidence in the reality of the relationships among these community-level parameters, it is reasonable to ask the nature of the relationships and the mechanisms that underlie them. The most productive test of the revised system model would

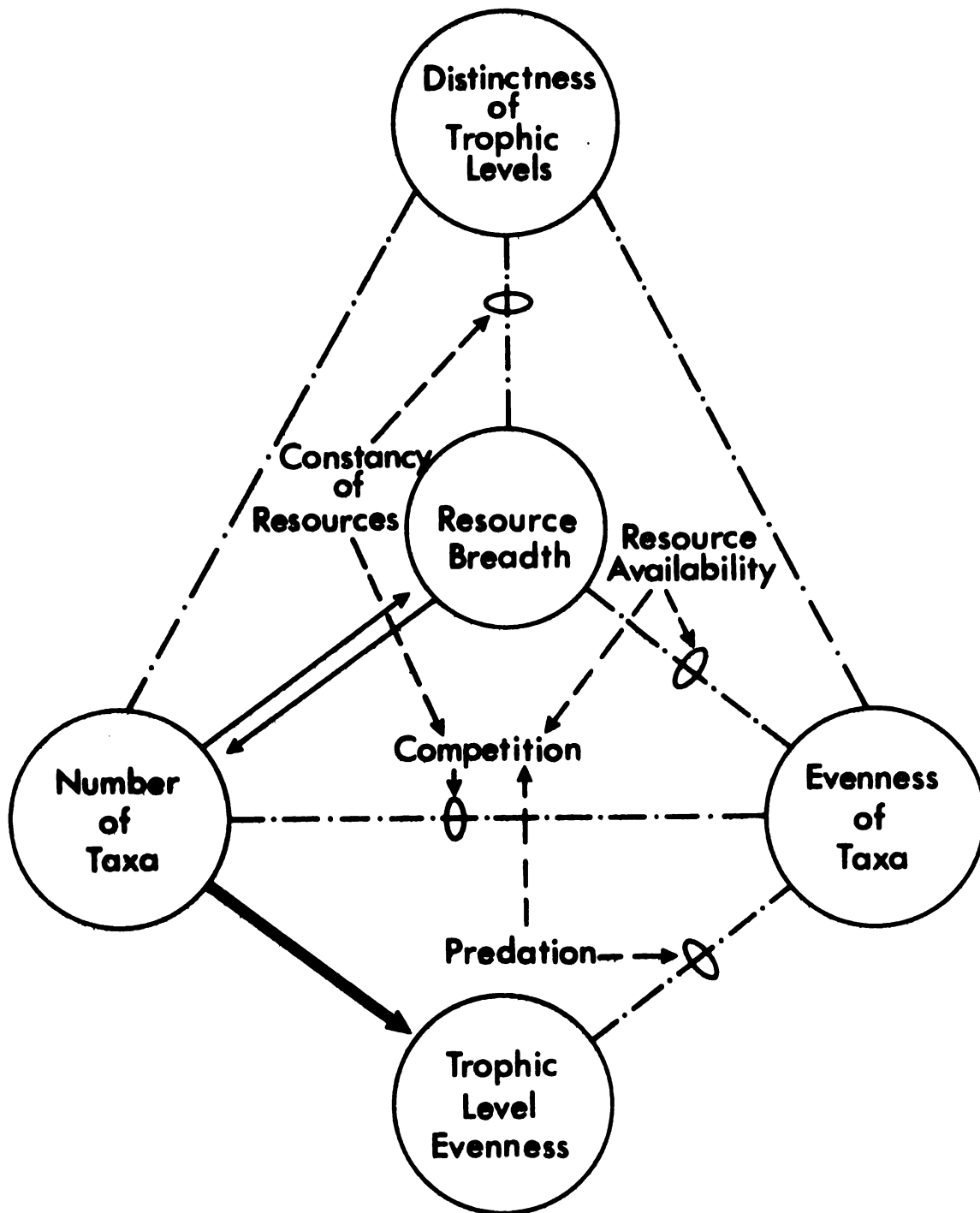


Figure 15. Revised System Model.



involve experimental manipulation of the parameters under controlled conditions. Controlled conditions are difficult to obtain with biological communities, and an alternative approach is to seek out just the "right" natural conditions where large numbers of parameters remain constant and few vary.

As testing these models progresses, additional parameters can be included in the system models, the free-body models of individual parameters can be refined, and the qualitative relationships discussed in this report can be replaced by quantitative relationships.

Up to the present, community level studies appear to have concentrated upon few parameters, their extent and mechanisms which may generate them. Discussion of relationships among community level parameters is rudimentary and generalized. The results of this study indicate that these relationships are complex and consistent and warrant further investigation.

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## SUMMARY AND CONCLUSIONS

Five parameters, Number of Taxa, Evenness of Taxa, Resource Breadth, Evenness of Trophic Levels, and Distinctness of Trophic Levels, are shown to be related to food-web structure. They are investigated from two points of view. First they are compared between islands and mainlands and through the summer growing season. Second, a model of expected relationships among the parameters is developed from review of literature, and ten predictions concerning correlation between parameters are drawn from this model and are tested experimentally.

- I. 1. Number of Taxa is lower in island than mainland communities, as would be expected from the theory of island biogeography.
2. Evenness of Taxa is higher on islands, possibly due to differential absence of rare taxa on depauperate islands. Evenness of Taxa is not influenced by summer season changes.
3. Resource Breadth may be influenced more by scale of sampling than by insularity or seasonality.
4. Evenness of Trophic Levels is higher on mainlands than on islands. Insularity may differentially influence population sizes of taxa at different trophic levels but not the numbers of taxa at those levels. Evenness of Trophic Levels decreased during the summer season in Ohio, probably because of a similar decrease in Number of Families of animals in Ohio, which would narrow the apex of an Eltonian pyramid.
5. The effect of insularity on Distinctness of Trophic Levels is reversed between Ohio and Michigan. Several alternative hypotheses to explain this reversal are presented. Distinctness of Trophic Levels increases during the summer season.

- II. 1. The general structure of the system model has withstood experimental test. The relationships modeled are complex, consistent, and warrant further investigation and search for mechanisms.
2. It is parsimonious and not invalid to hypothesize that Number of Taxa and Evenness of Taxa are related only by common but inverse correlation with other parameters such as insularity.
3. A negative relationship between Number of Taxa and Resource Breadth suggests the hypothesis that fugitive or opportunistic species are also the species with least Resource Breadth.
4. In communities where an Eltonian pyramid is not inverted, Evenness of Trophic Levels is inversely related to Number of Taxa of plants and directly related to Number of Taxa of animals.
5. It is tentatively concluded that Number of Taxa and Distinctness of Trophic Levels are related by common and direct correlation with factors of insularity.
6. A negative correlation between Evenness of Taxa and Distinctness of Trophic Levels suggests the hypothesis that animal taxa that do not clearly distinguish trophic levels in feeding also tend to be either rare or dominant or both.



## LIST OF REFERENCES

- Arnett, Ross H., Jr. (1960): The Beetles of the United States. Catholic University of America Press, Wash., D.C.
- Ares, J. O. and R. J. C. Leon (1972): An Ecological Assessment of the Influence of Grazing on Plant Community Structure. *J. Ecol.*, 60(2): 333-342.
- Arnold, S. J. (1972): Species Densities of Predators and their Prey. *Am. Nat.*, 106(948):220-236.
- Auclair, A. N. and F. G. Goff (1971): Diversity Relationships of Upland Forests in the Western Great Lakes Area. *Am. Nat.*, 105(946):499-528.
- Baker, R. H. (1971): Nutritional Strategies of Myomorph Rodents in North American Grasslands. *J. Mamm.*, 52(4):800-805.
- Beer, J. R., P. Lukens and D. Olsen (1954): Small Mammal Populations on the Islands of Basswood Lake, Minnesota. *Ecol.*, 35:437-445.
- Blatchley, W. S. (1920): Orthoptera of Northeastern America. The Nature Publishing Co., Indianapolis.
- Blatchley, W. S. (1926): Heteroptera or True Bugs of Eastern North America. The Nature Publ. Co., Indianapolis.
- Borror, D. J., and D. M. DeLong (1971): An Introduction to the Study of Insects, 3rd Edition. Holt, Rinehart, and Winston.
- Bristow, W. S. (1941): The Comity of Spiders, vol. II. London, Printed for the Ray Society.
- Bristow, W. S. (1958): The World of Spiders. Collins, St. James Place, London.
- Brown, J. (1972): Personal communication.
- Burch, J. B. (1962): How to Know the Eastern Land Snails. Wm. C. Brown Co., Dubuque, Iowa.
- Cameron, G. N. (1972): Analysis of Insect Trophic Diversity in two Salt Marsh Communities. *Ecol.*, 53(1):58-73.

- Caswell, H., H. E. Koenig, J. A. Resh, and Q. E. Ross (1972): An Introduction to Systems Science for Ecologists. In: B. C. Patten, ed., Systems Analysis and Simulation in Ecology. Academic Press, New York and London.
- Cloudsley-Thompson, J. L. (1939): Spiders, Scorpions, Centipedes and Mites. Pergamon Press, London.
- Colwell, R. K. and D. J. Futuyma (1971): On the Measurement of Niche Breadth and Overlap. *Ecol.*, 52(4):567-576.
- Connell, J. H. and E. Orias (1964): The Ecological Regulation of Species Diversity. *Am. Nat.*, 98(903):399-414.
- Crowell, K. L. (1961): The Effects of Reduced Competition in Birds. *Proc. Nat. Acad. Sci.*, 47:240-243.
- Crowell, K. L. (1962): Reduced Interspecific Competition among Birds of Bermuda. *Ecol.*, 43(1):75-88.
- Crowson, R. A. (1967): The Natural Classification of the Families of Coleoptera. E. W. Classey, Ltd., Middlesex, England.
- Curran, C. H. (1965): The Families and Genera of North American Diptera. Henry Tripp, Woodhaven, N.Y.
- Darnell, R. M. (1961): Trophic Spectrum of an Estuarine Community, Based on Studies of Lake Pontchartrain, Louisiana. *Ecol.*, 42:553-568.
- DeBenedictis, P. A. (1973): On the Correlations Between Certain Diversity Indices. *Am. Nat.*, 107(954):295-302.
- Downer, G. (1972): Personal Communication.
- Drew, L. C. (1967): Spiders of Beaver Island. Publications of the Museum, Mich. State U., Biol. Series, 3(3):153-208.
- Dwyer, P. D. (1973): Feature, Patch and Refuge Area: Some Influences on Diversity of Bird Species. *Emu*, 72(4):149-156.
- Ellis, A. R. (1969): British Snails. Oxford, Clarendon Press.
- Fedorov, A. A. (1966): The Structure of the Tropical Rain Forest and Speciation in the Humid Tropics. *J. Ecol.*, 54(1):1-11.
- Fitch, H. S. (1963): Spiders of the University of Kansas Natural History Reservation and Rockefeller Experimental Tract. U. of Kansas, Mus. of Nat. Hist., Misc. Pub. No. 33, pp. 1-202.
- Fleming, T. H. (1973): Numbers of Mammal Species in North and Central American Forest Communities. *Ecol.*, 54(3):555-563.
- Futuyma, D. J. (1973): Community Structure and Stability in Constant Environments. *Am. Nat.*, 107(955):443-445.

- Garfinkel, D. and R. Sack (1964): Digital Computer Simulation of an Ecological System, Based on a Modified Mass Action Law. *Ecol.*, 45(3):502-507.
- Gertsch, W. J. (1949): American Spiders. New York.
- Graham, A. (1955): Molluscan Diets. *Proc. Malac. Soc. London*, 31:144-157.
- Grant, P. R. (1966): Ecological Compatibility of Bird Species on Islands. *Am. Nat.*, 100(914):451-462.
- Grant, P. R. (1968): Bill Size, Body Size and the Ecological Adaptation of Bird Species to Competitive Situation on Islands. *Sys. Zool.*, 17:319-333.
- Hairston, N. G. (1959): Species Abundance and Community Organization. *Ecol.*, 40:404-416.
- Hairston, N. G., J. D. Allan, R. K. Colwell, D. J. Futuyma, J. Howell, M. D. Lubin, J. Mathias and J. H. Vandermeer (1968): The Relationship Between Species Diversity and Stability: An Experimental Approach with Protozoa and Bacteria. *Ecol.*, 49(6): 1091-1100.
- Hamilton, T. H. and N. E. Armstrong (1965): Environmental Determination of Insular Variation in Bird Species Abundances in the Gulf of Guinea. *Nature*, 207:148-151.
- Hamilton, T. H., R. N. Barth and I. Rubinoff (1964): The Environmental Control of Insular Variation in Bird Species Numbers. *Proc. U. S. Nat. Acad. Sci.*, 52:132-140.
- Heatwole, H. and R. Levins (1972): Trophic Structure Stability and Faunal Change During Recolonization. *Ecol.*, 53(3):531-534.
- Heatwole, H. and R. Levins (1973): Biogeography of the Puerto-Rican Bank: Species Turnover on a Small Cay, Cayo Ahogado. *Ecol.*, 54(5): 1042-1055.
- Hill, M. O. (1973): Diversity and Evenness: A Unifying Notation and its Consequences. *Ecol.*, 54(2):427-433.
- Hubbell, S. P. (1973): Populations and Simple Food-Webs as Energy Filters: I. One-Species Systems. *Am. Nat.*, 107(953):94-121.
- Hubbell, S. P. (1973): Populations and Simple Food Webs as Energy Filters. II. Two Species Systems. *Am. Nat.*, 107(953):122-151.
- Hurd, L. E., M. V. Mellinger, L. L. Wolf and S. J. McNaughton (1971): Stability and Diversity at Three Trophic Levels in Terrestrial Successional Ecosystems. *Science*, 173:1134-1136.



- Hurlbert, S. H., M. S. Mulla and H. R. Willson (1972): Effects of an Organophosphorus Insecticide on the Phytoplankton, Zooplankton, and Insect Populations of Fresh-Water Ponds. *Ecol. Monogr.*, 42(3): 269-299.
- Hurlbert, S. H., J. Zedler, and D. Fairbanks (1972): Ecosystem Alteration by Mosquito Fish (Gambusia Affinis) predation. *Science*, 175:639-641.
- Hutchinson, G. E. (1959): Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals? *Am. Nat.*, XCIII:145-159.
- Janzen, D. (1970): Herbivores and the Number of Tree Species in Tropical Forests. *Am. Nat.*, 104:501-528.
- Janzen, D. H. (1973): Sweep Samples of Tropical Foliage Insects: Effects of Seasons, Vegetation Types, Elevation, Time of Day, and Insularity. *Ecol.*, 54(3):687-708.
- Janzen, D. H. and T. W. Schoener (1968): Differences in Insect Abundances and Diversity between Wetter and Drier Sites during a Tropical Dry Season. *Ecol.*, 49(1):96-109.
- Johnson, R. G. (1970): Variations in Diversity within Benthic Marine Communities. *Am. Nat.*, 104:285-300.
- Johnson, M. P., L. G. Mason and P. H. Raven (1968): Ecological Parameters and Plant Species Diversity. *Am. Nat.*, 102:297-306.
- Johnson, M. P. and P. Raven (1970): Natural Regulation of Plant Species Diversity. pp. 127-162 in: Evolutionary Biology, ed. by Dobzhansky, Hecht and Steere, vol. 4. Appleton-Century-Crofts.
- Kaston, B. J. (1972): How to Know the Spiders. Wm. C. Brown Co., Dubuque, Iowa.
- Keast, A. (1970): Adaptive Evolution and Shifts in Niche Occupation in Island Birds. *Biotropica*, 2(2):61-75.
- Kendall, M. G. and A. Stuart (1967): The Advanced Theory of Statistics, vol. 2. Hafner Pub. Co., N.Y.
- Kilburn, P. D. (1966): Analysis of the Species-Area Relation. *Ecol.*, 47(5):831-843.
- Klopfer, P. H. and R. H. MacArthur (1961): On the Causes of Tropical Species Diversity in Niche Overlap. *Am. Nat.*, 95:223-226.
- Kohn, A. J. (1967): Environmental Complexity and Species Diversity in the Gastropod Genus Conus on Indo-West Pacific Reef Platforms. *Am. Nat.*, 101:251-259.
- Kricher, J. C. (1972): Summer Bird Species Diversity in Relation to Secondary Succession on the New Jersey Piedmont. *Am. Midl. Nat.*, 89(1):121-137.

- Leigh, E. G., Jr. (1965): On the Relation Between the Productivity, Biomass, Diversity, and Stability of a Community. *Proc. N. A. S.*, 53:777-783.
- Leonard, A. B. (1959): Handbook of Gastropods in Kansas. U. of Kansas, Mus. of Nat. Hist., Misc. Pub. No. 20, pp. 1-224.
- Levins, R. (1968): Evolution in Changing Environments. Princeton University Press, Princeton, N. J.
- Levinton, J. (1972): Stability and Trophic Structure in Deposit-Feeding and Suspension-Feeding Communities. *Am. Nat.*, 106(950):472-486.
- Loucks, O. L. (1970): Evolution of Diversity, Efficiency and Community Stability. *Am. Zool.*, 10:17-25.
- MacArthur, R. H. (1964): Environmental Factors Affecting Bird Species Diversity. *Am. Nat.*, 98:387-397.
- MacArthur, R. H. (1965): Patterns of Species Diversity. *Biol. Rev.*, 40:510-533.
- MacArthur, R. H. (1969a): Patterns of Communities in the Tropics. *Biol. J. Linn. Soc.*, 1:19-30.
- MacArthur, R. H. (1969b): Species Packing, and What Interspecies Competition Minimizes. *Proc. of the Nat. Acad. of Sci.*, 64(4): 1369-1371.
- MacArthur, R. H. (1970): Species Packing and Competitive Equilibrium for Many Species. *Theor. Pop. Biol.*, 1(1):1-11.
- MacArthur, R. H. (1972) Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, Publishers.
- MacArthur, R. H., J. M. Diamond and J. R. Karr (1972): Density Compensation in Island Faunas. *Ecol.*, 53(2):330-342.
- MacArthur, R. H. and R. Levins (1964): Competition, Habitat Selection and Character Displacement in a Patchy Environment. *Proc. Nat. Acad. Sci.*, 1:1207-1210.
- MacArthur, R. H. and R. Levins (1967): The Limiting Similarity, Convergence and Divergence of Coexisting Species. *Am. Nat.*, 101: 377-385.
- MacArthur, R. H., J. MacArthur, D. MacArthur and A. MacArthur (1973): The Effect of Island Area on Population Densities. *Ecol.*, 54(3): 657-658.
- MacArthur, R. H. and M. C. Recher (1966): On the Relation Between Habitat Selection and Species Diversity. *Am. Nat.*, 100:319-332.

- MacArthur, R. H. and E. O. Wilson (1963): An Equilibrium Theory of Insular Zoogeography. *Evol.*, 17(4):373-387.
- MacArthur, R. H. and E. O. Wilson (1967): Theory of Island Biogeography. Princeton, N. J., Press.
- Mackay, R. and J. Kalff (1969): Seasonal Variation in Standing Crop and Species Diversity of Insect Communities in a Small Quebec Stream. *Ecol.*, 50(1):101-109.
- Maguire, B., Jr. (1967): A Partial Analysis of the Niche. *Am. Nat.*, 101:515-526.
- Mahler, J. (1972): Personal communication.
- Malone, C. R. (1972) Effects of a Non-Selective Arsenical Herbicide on Plant Biomass and Community Structure in a Fescue Meadow. *Ecol.*, 53(3):507-512.
- Margalef, R. (1967): Some Concepts Relative to the Organization of Plankton. *Oceanogr. Mar. Biol. Ann. Rev.*, 5:257-289.
- M'Closkey, R. T. (1972): Temporal Changes in Populations and Species Diversity in a California Rodent Community. *J. Mamm.*, 53(4):657-676.
- McPherson and J. N. Krull (1972): Island Populations of Small Mammals and Their Affinities with Vegetation Type, Island Size and Distance from Mainland. *Am. Midl. Nat.*, 88:384.
- Morse, D. H. (1971): The Foraging of Warblers Isolated on Small Islands. *Ecol.*, 52(2):216-228.
- Murdoch, W. W., F. C. Evans and C. H. Peterson (1972): Diversity and Pattern in Plants and Insects. *Ecol.*, 53(5):819-829.
- Nie, N. H., D. H. Bent and C. H. Hull (1970): Statistical Package for the Social Sciences. McGraw-Hill Book Co.
- Odum, E. P. (1969): The Strategy of Ecosystem Development. *Science*, 164:262-270.
- Oldroyd, H. (1964): The Natural History of Flies. Weidenfield and Nicolson, London.
- Qrians, G. H. (1969): The Number of Bird Species in Some Tropical Forests. *Ecol.*, 50(5):783-801.
- Paine, R. T. (1966): Food Web Complexity and Species Diversity. *Am. Nat.*, 100(910):65-76.
- Parrish, J. D. and S. B. Saila (1970): Interspecies Competition, Predation and Species Diversity. *J. Theor. Biol.*, 27(2):207-220.



- Pearson, D. L. (1971): Vertical Stratification of Birds in a Tropical Dry Forest. *The Condor*, 73:46-55.
- Phillip, J. R. (1957): Sociality and Sparse Populations. *Ecol.*, 38(1): 107-111.
- Pianka, E. R. (1966): Latitudinal Gradients in Species Diversity: A Review of Concepts. *Am. Nat.*, 100(910):33-46.
- Pianka, E. R. (1967): On Lizard Species Diversity: North American Flatland Deserts. *Ecol.*, 48(3):333-351.
- Pianka, E. R. (1969): Habitat Specificity, Speciation and Species Density in Australian Desert Lizards. *Ecol.*, 50:498-502.
- Pielou, E. C. (1966): Species-Diversity and Pattern-Diversity in the Study of Ecological Succession. *J. Theor. Biol.*, 10:370-383.
- Pielou, E. C. (1969): An Introduction to Mathematical Ecology. Wiley-Interscience.
- Pielou, E. C. (1972): Niche Width and Overlap: A Method for Measuring Them. *Ecol.*, 53(4):687-692.
- Porter, J. W. (1972a): Predation by Acanthaster and its Effect on Coral Species Diversity. *Am. Nat.*, 106(950):487-492.
- Porter, J. W. (1972b): Patterns of Species Diversity in Caribbean Reef Corals. *Ecol.*, 53(4):745-748.
- Power, D. (1972): Numbers of Bird Species on the California Islands. *Evol.*, 26(3):451-563.
- Preston, F. W. (1962a): The Canonical Distribution of Commonness and Rarity, I. *Ecol.*, 43:185-215.
- Preston, F. W. (1962b): The Canonical Distribution of Commonness and Rarity, II. *Ecol.*, 43:410-432.
- Pulliam, H. R., E. P. Odum and G. W. Barrett (1968): Equitability and Resource Limitation. *Ecol.*, 49:772-774.
- Purchon, R. D. (1968): The Biology of the Mollusca. Pergamon Press.
- Reiners, W. A., I. Wooly and D. B. Lawrence (1971): Plant Diversity in a chronosequence at Glacier Bay, Alaska. *Ecol.*, 52:55-69.
- Ricklefs, R. E. and G. W. Cox (1972): Taxon Cycles in the West Indian Avifauna. *Am. Nat.*, 106(948):195-219.
- Rohlf, F. J. and R. R. Sokal (1969): Statistical Tables. W. H. Freeman and Company, San Francisco.

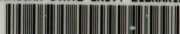
- Rosenzweig, M. L. (1973): Exploitation in Three Trophic Levels. *Am. Nat.*, 107(954):275-294.
- Schoener, T. W. (1968): The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. *Ecol.*, 49(4):704-724.
- Schoener, T. W. (1969): Size Patterns in West Indian Anolis lizards; I. Size and Species Diversity. *Sys. Zool.*, 18:386-401.
- Shannon, C. E. and W. Weaver (1949): The Mathematical Theory of Communication. University of Illinois Press, Urbana.
- Sheldon, A. L. (1968): Species Diversity and Longitudinal Succession in Stream Fishes. *Ecol.*, 49(2):193-198.
- Sheldon, A. L. (1969): Equitability Indices: Dependence on the Species Count. *Ecol.*, 50(3):466-467.
- Sheppard, D. H., P. H. Klopfer and H. Oelke (1968): Habitat Selection: Differences in Stereotypy Between Insular and Continental Birds. *Wilson Bull.*, 80(4):452-457.
- Shugart, H. H. and B. G. Blaylock (1973): The Niche-Variation Hypothesis: An Experimental Study with Drosophila populations. *Am. Nat.*, 107(956):575-579.
- Simberloff, D. S. (1969a): Taxonomic Diversity of Island Biotas. *Evol.*, 24:23-47.
- Simberloff, D. S. (1969b): Experimental Zoogeography of Islands, III. *Ecol.*, 50(2):296-314.
- Simberloff, D. S. and E. O. Wilson (1969): Experimental Zoogeography of Islands II. *Ecol.*, 50(2):278-295.
- Slobodkin, L. B. and H. L. Sanders (1969): On the Contribution of Environmental Predictability to Species Diversity. In Diversity and Stability in Ecological Systems. Brookhaven Sym. in Biol., No. 22, pp. 82-95.
- Sokal, R. R. and F. J. Rohlf (1969): Biometry. W. H. Freeman and Co., San Francisco.
- Soulé, M. (1970): Response to Van Valen, L. and P. R. Grant. *Am. Nat.*, 104(940):590.
- Soulé, M. and B. R. Stewart (1970): The "Niche-Variation" Hypothesis: A Test and Alternatives. *Am. Nat.*, 104(935):85-97.
- Spight, T. G. (1967): Species Diversity: A Comment on the Role of the Predator. *Am. Nat.*, 101:467-474.
- Stephenson, J. (1930): The Oligochaeta. Clarendon Press.

- Stonerook, Mrs. P. (1972): Personal communication.
- Teal, J. M. (1962): Energy Flow in the Salt Marsh Ecosystem of Georgia. *Ecol.*, 43(4):614-624.
- Terborgh, J. (1971): Distribution on Environmental Gradients: Theory and a Preliminary Interpretation of Distributional Patterns in the Avifauna of the Cordillera Vilcabamba, Peru. *Ecol.*, 52(1):23-40.
- Tramer, E. J. (1969): Bird Species Diversity: Components of Shannon's Formula. *Ecol.*, 50(5):927-929.
- Vandermeer, J. H. (1970): The Community Matrix and the Number of Species in a Community. *Am. Nat.*, 104(935):73-83.
- Van Name, W. G. (1936): The American Land and Freshwater Isopod Crustacea. *Bull. Amer. Mus. Nat. Hist.*, 71:1-535.
- Van Valen, L. (1965): Morphological Variation and Width of Ecological Niche. *Am. Nat.*, XCIX(908):377-390.
- Van Valen, L. and P. R. Grant (1970): Variation and Niche Width Re-Examined. *Am. Nat.*, 104(940):589-590.
- Vuilleumier, F. (1972): Bird Species Diversity in Patagonia (Temperate South America). *Am. Nat.*, 106(948):266-271.
- Whitehead, R. R. and C. E. Jones (1969): Small Islands and the Equilibrium Theory of Insular Biogeography. *Evol.*, 23(1):171-180.
- Whiteside, M. C. and R. V. Harmsworth (1967): Species Diversity in Chydorid (Cladocera) Communities. *Ecol.*, 48(4):664-668.
- Wiegert, R. G. and D. F. Owen (1971): Trophic Structure, Available Resources and Population Density in Terrestrial versus Aquatic Ecosystems. *J. Theor. Biol.*, 30:69-81.
- Williams, E. E. (1969): The Ecology of Colonizing Species as Seen in the Zoogeography of Anoline Lizards on Small Islands. *Quart. Rev. of Biol.*, 44(4):345-389.
- Willson, M. F. (1969): Avian Niche Size and Morphological Variation. *Am. Nat.*, 103:531-542.
- Wilson, E. O. (1969): The Species Equilibrium. In: Diversity and Stability in Ecological Systems. Brookhaven Symp. in Biol., No. 22, pp. 38-47.
- Wilson, E. O. and D. S. Simberloff (1969): Experimental Zoogeography of Islands, I. *Ecol.*, 50(2):267-277.
- Wilson, E. O. and R. W. Taylor (1967): An Estimate of the Potential Evolutionary Increases in Species Density in the Polynesian Ant Fauna. *Evol.*, 21(1):1-11.

Wilson, K. V. (1956): A Distribution-Free Test of Analysis of Variance Hypotheses. Psychological Bull., 53(1):96-101.



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