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Proceedings: Conference on Applications of the Guild Concept to Environmental Management

Edited by
William D. Severinghaus
Terry D. James

This report provides the proceedings of the conference held on 20-22 April 1982, sponsored by the University of Illinois and the U.S. Army Corps of Engineers, to discuss the philosophy within basic and applied ecology of classifying organisms into functional units (guilds). The meeting was attended by a cross-section of scientists representing state and Federal government agencies, academic institutions, and private enterprise.

The major points raised during the conference were (1) the imprecision of the concept of guild classification within and between academic and applied ecological research communities, (2) the need for functional classification to help define problems and analyze management goals, (3) the potential for the guild concept in applied ecological research, and (4) the premature status of statistical procedures for using the guild concept in applications-oriented studies.

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This report provides the proceedings of the conference held on 20-22 April 1982 and sponsored by the University of Illinois and the U.S. Army Corps of Engineers to discuss the philosophy within basic and applied ecology of classifying organisms into functional units (guilds). The meeting was attended by a cross-section of scientists representing state and Federal government agencies, academic institutions, and private enterprise.

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The first part of the conference was devoted to discussing (1) the need for functional classification in ecology (as compared to taxonomic or phylogenetic classification), (2) the development and meaning of the guild concept, and (3) the manner in which it is interpreted by the academic community. The formal presentations crossed the general fields of entomology, botany, herpetology, ornithology, ecology, and evolution. Subsequent discussion centered on discrepancies between the definition of a guild and the manner in which the concept is being interpreted. Although there was no general agreement on the definition or appropriate use of the term "guild," it was agreed that individual scientists undertaking functional classification and using the term "guild" should clearly define their use of the term, including the purpose for their classification.

The second portion of the conference dealt with use of guild classifications within the "classical" management disciplines of forestry and wildlife management. The presentations concentrated on birds, with discussions of "guild block" matrices, guild indicator versus guild unit approaches, and guild density. The usefulness of guilds as a clustering tool for monitoring, the advantages of the "unit" approach, and the ability of guild-based studies to discern change at various temporal and spatial scales were discussed.

The third session dealt with application of the guild concept to contemporary problems of environmental monitoring and management. The need for biological monitoring in combination with physical and chemical monitoring was stressed; use of the guild concept in the form of community guild signature (percent distribution of guilds) was discussed as a key component of biological monitoring programs. The development of an "index of biotic integrity" and the importance of species lists were also discussed. Soils and plants, as they pertain to the uniqueness of reclamation, nature preserves, and the problems of applying ecological generalizations across a wide variety of site-specific problems were examined.

The final session provided discussion of several research programs that use the guild concept. Formal presentations dealt with the use of guild-based classification schemes in environmental analysis, prediction and mitigation, use of computerized databases for guild membership delineation, and use of the guild concept in examining hazardous and toxic waste pathways through ecosystems.

The major points raised during the conference were (1) the imprecision of the concept of guild classification within and between academic and applied ecological research communities, (2) the need for functional classification to help define problems and analyze management goals, (3) the potential for the guild concept in applied ecological research, and (4) the premature status of statistical procedures for using the guild concept in applications-oriented studies.

FOREWORD

This publication was funded by the Directorate of Civil Works, Office of the Chief of Engineers (OCE) under Work Unit Number CWIS 32230, "Guild-Based Model for Environmental Assessment and Evaluation." The OCE Technical Monitors were Drs. John Belshé and John Bushman DAEN-CWP-P.

The conference documented in this publication was coordinated by Dr. William D. Severinghaus, Environmental Division (EN), U.S. Army Construction Engineering Research Laboratory (USA-CERL). The conference was sponsored by the University of Illinois and the U.S. Army Corps of Engineers.

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OPENING REMARKS

Dr. John Belshé Chief, Environmental
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To open this workshop, I would like to briefly discuss: (1) the Corps of Engineers; (2) the background on this meeting; (3) some of the goals that we hope to accomplish; (4) the audience; and (5) my own perspectives on the meeting.

Some people think of the Corps of Engineers as only a construction agency, but it is also a land management agency. The Corps directly controls about 12 million acres of U.S. property which is, on the whole, fairly low in elevation, good land along our rivers or around navigational ports. The Corps also, through consultation, frequently has an impact on about an equal amount of acreage in military bases. Of additional interest are those properties that the Corps is considering acquiring, or properties on which it might be doing a water resource program for operation by local interests. All this is what brings us into resource management. Such work is performed by about 500 environmental scientists concerned with planning, 400 involved in natural resource management, and more than 200 in the six Corps research laboratories.

We apply the principles of habitat, or wildlife management, in many aspects of the work we do in planning, design, construction, operation and maintenance. Our interest in guilding—the subject of this conference—comes from a recognition that a knowledge of habitat, evaluation of that habitat, and management from a habitat perspective, are very important to doing good planning and design work.

The Corps of Engineers is organized into two programs: military and civil works. My office is part of the civil works program, and much of what I have said about our perspective on land management originates from that civil component. But it is the military program that leads me to a discussion of how this meeting evolved.

About August 1980, it came to our attention that the Construction Engineering Research Laboratory (CERL) had been doing some work with ecological guilds, and that the U.S. Fish and Wildlife Service was doing similar studies. Because of our habitat evaluation interests, it seemed prudent to look for applications of this concept to civil works activities. Also at that time, the Waterways Experiment Station (WES) was about to begin research on habitat evaluation methodologies to better interface with activities already underway in the Fish and Wildlife Service. This interface was to take the Fish and Wildlife Service's findings and direct them toward Corps applications. We hoped to build an infrastructure which could provide assistance in habitat evaluation or management available to the field.

If there is information to be shared, or techniques to be considered and perhaps adopted, then a technology transfer workshop can be considered. What goals did we set for such an undertaking? I think we essentially set two which remain valid. First, there is certainly an information transfer

component that you collectively brought to this review, and such an exchange of knowledge can make this workshop a state-of-the-art review for all concerned. Second, this was a good opportunity for a strong representation from the Corps field elements (district and division offices) to ensure that they have a full understanding of the state-of-the-art methodology, based on sound, conceptual foundations and adhering to fairly strict use of the scientific terminology. Please do not lose sight of either of those aspects: the state-of-the-art review and the tutorial opportunity. The civil works component is looking to this program, which began within the military component, to decide if more research is needed; and, if so, the particular type required for its purposes. We want to use this meeting as a scoping medium, not only to identify researchable items, but also to develop a realistic way to achieve such objectives.

We essentially have brought four groups together here. The first is the Corps people. With today's budget problems and changing direction, they should recognize that to keep in step with our planning improvement program, some new ways or procedures, such as guild theory, may help us do our job better and be more cost-effective and timely.

A second group represented here is other Federal agencies; certainly their technology transfer role is very important. We want to know the best of what you are doing, that you are aware of what we are doing, and that we can jointly move to do our jobs in an efficient and meaningful way for the Federal Government.

A third group represents the academic community, and I view your leadership, and your role, in science as very real and very immediate. We are very plesed that you have joined us in the numbers that you have. We believe the program should, therefore, reflect some of the best state-of-the-art advice that the academic community can provide.

Finally, we recognize our hosts--personnel from CERL--whose job is to identify and scope out further research work in such a way that management action can be taken.

I have a strong interest in more efficient, cost-effective, management. This meeting may help to bridge a gap between what could be called the deterministic approach and the sort of stochastic engineering that goes into our water resources program. The younger staff members, coming to the U.S. Army Corps of Engineers from universities, are prepared to treat wildlife or biological problems as a cause and effect problem. But, when one gets into the area of environmental impact, one is really talking about the risks of an engineering undertaking, and the resources for approaching the problem in a causal way are often not available. We must turn back to look at the extremes of variation; we cannot look for point-by-point continuity, and deterministic relationships. We have to try to see what the range of response may be, and then be sure that we feel comfortable when we have reduced the risk inherent in the undertaking to some manageable level. It may not be the perfect response; it's certainly not the no-risk situation. But we have brought the best of our science and engineering to the task of reducing that risk to something that is manageable. Then we can internalize our evaluation and decide whether that project should be scrutinized from something like a benefit-cost methodology, or a risk-benefit methodology.

Guilding holds promise in helping to focus our attention on key variables and in helping reduce the large number of variables that may seem needed when planning for water projects in a particular area. I also think guilding considerations may reduce the environmental components to be investigated and help us select those that should be presented to other scientists and engineers. Those we present should best illustrate the responses, the impacts, and the predictions that are needed by the decision-maker. The decision-maker may be acting on a report describing a proposed Federal undertaking in response to a congressional study resolution. None of those levels (the agency, the administration, or the congress) is well served by abstraction. All need something tangible. A great virtue in the area of wildlife and other biological studies is that they can be very tangible. We must represent our biological opinions in meaningful ways, and back them with a carefully selected set of numbers. The guild theory appears to offer progress toward that goal.

SESSION I: THE NEED, ORIGIN, AND THEORETICAL USE OF THE GUILD THEORY

INTRODUCTION

William D. Severinghaus, U.S. Army Construction Engineering
Research Laboratory, Champaign, IL

In this first session I hope we can communicate some things that are going on in academia and how the ecological aspect of guilding got started. Right now it's being used (and, some people feel, abused) in many different ways. I hope this session will bring home how it got started and how it was originally meant to be used, and if we want to argue about how it's used by other people, we can do that too.

Several years ago, I heard Sydney Anderson (American Museum of Natural History) make a presentation on how ideas get proliferated in the scientific literature. He indicated that it takes about 7 years from the time something is published until it is well used, and it takes about another 7 years before people stop using it. I did a search from several of the abstracting services to determine how many publications have mentioned guilds in some way. The first publication on guilding by Dr. Root was in 1967 (Ecological Monographs, 37:317-350), and it was 1974 before the topic was picked up. From one publication in 1974 it rose to 33 in 1980. Also of interest is that most of these publications were about birds and insects. The use of guilds is not going to die out after 7 years.

Topics that this session will cover are: the definition of a guild; how scientists are using the theory; and whether guilds are delineated only by resource utilization (some papers refer to morphological guilds and there are several other ways it's being used). During this first session, we will see how the guild is being used and why it was devised.

FUNCTIONAL CLASSIFICATION AND THE DEVELOPMENT OF THE GUILD CONCEPT

Richard B. Root, Cornell University, Ithaca, NY

Today, I want to discuss the guild concept in the broad context that concerns people who are interested in characterizing ecosystems in communities and measuring the impacts of organisms or perturbations on these systems. None who work in ecology need to be reminded that one of the great difficulties we confront is the extreme complexity of the natural systems. This complexity greatly hinders our ability to observe basic processes, to make generalizations, and to understand impact.

Let me start by recalling the level of complexity that ecologists encounter when they investigate an entire ecosystem. For instance, Evans and Murdock, working in an old field in Michigan, found 1584 species of insects belonging to 179 families. The insects, of course, are only one component of the community. In work that we did on the insects associated with collards-- as homogeneous an ecosystem as you can imagine--there were 99 species of herbivorous insects belonging to 22 families, and 103 species of parasitoid wasps belonging to 14 families. This kind of complexity severely limits our ability to penetrate the basic underlying processes in the system. It's one of the things that makes ecology so interesting, so challenging, and so difficult.

This complexity confronts us in yet another way. When we try to address questions relating to an entire system, we are limited in our ability to properly sample all of the elements it contains. For instance, one of my classes sampled the insect fauna of an old field using a sweep net and a D-vac. We contrasted the insects that we had encountered by these two sampling methods and found they produced totally different communities! The community inferred from the sweep net was heavily dominated by grasshoppers; the community inferred from the D-vac (vacuum-collecting net) was dominated by sap-feeding insects. This experience is repeated in a diversity of systems and shows that when we address whole systems, there is no single sampling method that is appropriate for major segments of the biota. Because species differ so greatly in their sampleability, there are either larger biases in our methods or the analysis is extremely expensive.

Ecologists have responded to this complexity in a number of ways. One way is to assemble large teams, as was done during the International Biological Program period. However, hundreds of people, all trying to work together, present an enormous difficulty. In particular, when a huge team is required to deal with the complexity of a system, it is difficult for one person to keep the final synthesis of the study in mind, and many critical, but subtle, factors may be missed. By far, the most frequently used procedure for reducing complexity is to subdivide the system--to simplify the problems by focusing on more manageable units. This procedure of dividing up the system involves much of the "art" in ecology, and we will see that many of the greatest blunders in our field can ultimately be traced to situations in which somebody has chosen inappropriate units. Discussing this art and the various schemes (not just guild identification) that are used to reduce complexity brings us to the broad issue of functional classifications.

The phylogenetic taxon provides the most popular category for those attempting to simplify a system--for example, limiting consideration to the butterfly, the bird, or the copepod community. Unfortunately, except in the case of plants (which constitute an entire trophic level), such communities rarely have any functional reality and, indeed, most taxon-defined communities are really fragments of several functional systems. Thus, when we discuss a bird community, we group together sparrows and hawks, but ignore, for example, mice and ants that would eat the same food as sparrows. By combining into one category (a taxon unit) several functional systems that are not necessarily related, and ignoring other aspects of the system that might be important in their interactions, many of the important factors that should be organizing the system may be obscured. But we are fundamentally interested in these organizing factors because, if we are going to tamper with nature, we must understand how the system is organized. Thus, if competition between very different organisms were the critical organizing principle in a system, our conclusions would be entirely wrong if we were to restrict our view only to one taxon.

Taxonomic studies obviously are of interest in ecology because they deal directly with evolutionary questions. They were the source of many of our early insights. However, they are inadequate for many questions that involve processes. For these, we require more functional concepts, truly ecological constructs, which are uncoupled from the phylogenetic concerns that define taxa. Basically, I feel there are three general types of concepts that can be used in functional classifications.

The first of these is the life-form concept, which is based on the shared adaptations of organisms within the system. The second is the guild, which is based on the functional role that species perform in a community. The guild is particularly useful in trying to understand aspects of the system's horizontal organization (e.g., the species diversity within a trophic level). Finally, there is the component community or component system which is a subdivision that incorporates the vertical structure of the community and provides a workable unit for the study of trophic webs. There is not time to discuss this latter concept and I will merely refer those with an interest to my paper (1973) in Ecological Monographs. Studies of all these units have validity in their own right. Each provides an alternative scheme that the investigator must select to pare down the complexity of nature so that one person can comprehend what is happening. The art lies in selecting the correct scheme.

The life-form concept groups species according to their similarity with respect to a particular adaptation. This concept originated in Europe, where it was the focus of much of the early research in ecology. The Danish botanist, Raunkaier, developed a scheme for classifying plants based on position of the perenniating bud (growth point) during the adverse season. Raunkaier then gathered data on different kinds of communities and made inferences about how physical conditions structured the vegetation. This idea has been extended into studies in which plants have been classified by dispersal types. In the European literature, the zoologists have begun to look at other aspects of species biology, e.g., methods of overwintering in insects or adaptations for avoiding predators. The value of the life-form concept is that it permits classification of biota with respect to the response to various kinds of stresses. Once such a classification has been

made, it is then possible to compare different communities, or to compare the same community under different kinds of impact in such a way that one gains insight about how a particular factor (e.g., exposure to wind, action of grazers, etc.) molds the biota. This approach has been around a long time, but has generally been neglected in American.

Understanding many aspects of community organization requires a unit that groups species according to their functional roles. This was what I had in mind when I coined the term "guild," which I define as "a group of species that exploits the same class of environmental resources in a similar way." Why did I choose this particular definition and what are some of its implications? First note that the guild is not restricted to a particular taxonomic group. As a result, we have a functional group divorced from phylogenetic consideration. For example, several insect families belonging to four separate orders (Coleoptera, Hymenoptera, Lepidoptera, and Diptera) burrow out mines in leaves. Thus, this functional mode of life has been available to many species that are not closely related to one other, but which potentially can have a heavy impact on each other. Another even more restricted example involves the insects that form stem galls on goldenrod. Here there are four genera in two orders that utilize the same host; thus, there are at least four different adaptive or evolutionary pathways resulting in the utilization of the same portion of the same plant. This is one of the main reasons for not restricting guilds taxonomically. I was particularly interested in getting rid of the taxonomic bias, because there had been a tendency to study interspecific competition within congenors. This is an idea that stemmed from Darwin, and may be one of the few areas in which Darwin led us somewhat astray. He postulated that the most intense competition should take place between the most closely related species. While this is true, in a sense, not all significant competition is limited to the most closely related species. To examine the full spectrum of competitive interactions, it is necessary to look beyond the genus. To examine the full spectrum of competitive interaction, it is necessary to look beyond the genus. It seemed to me that the guild would define a unit that better reflected the outcome of competitive interaction. While this was one of my major reasons for proposing the guild concept, of even greater importance was the fact that there was complete confusion surrounding the niche concept at that time.

Grinnell was the first to put forth the niche concept, but little attention was paid to it. Grinnell's concept of the niche was also different from what others proposed. Elton, writing in 1927, was the first to discuss the niche in terms that really came into broad usage. I want to trace this history a little, because it is important in understanding the conceptual origins of a number of things that we are discussing. He wrote, "The niche of an animal means its place in the biotic environment, its relation to food and enemies." He went on to say that when an ecologist says, "There goes the badger," he should include in his thoughts some definite idea of the animal's place in the community, much as he would think were he to say "There goes the vicar." Elton had in mind an idea of an occupation--the species' functional role in the community. Elton continued by saying that the importance of studying the niche is partly that it enables us to see how very different communities may resemble each other in the essentials of organization. He saw "niche" as an idea having to do with the organization of communities. For instance, there is a niche which is filled by birds of prey that eat small mammals, such as shrews and mice. In an oak wood, this niche is filled by

tawny owls, while in the open grassland, it is occupied by kestrels. In other words, he was really defining a functional role, and it is not linked to any particular community.

Later there was a big push toward mathematical ecology. Many mathematical models about interspecific competition were developed, and some experiments were done that led some people to think that there was a close correspondence between the models and nature. Later others, particularly David Lack, in attempting to relate the mathematics to more naturalist terms, came up with statements of the general form: "No two species can occupy the same niche." As a result, the idea of "niche" became linked with the competitive exclusion principle. Obviously, the niche has much to do with competition, but the simple linkage embroiled the niche concept in the debate about the validity of the competitive exclusion principle and caused semantic confusion. Out of this semantic confusion came, in 1957, a new definition of the niche by MacFadyen, working in England, and, independently, by Hutchinson, working in the United States. According to the Hutchinson-MacFadyen definition, a niche is a set of conditions that permits a species to exist indefinitely. The niche thus became an abstract space in the environment that a species must be able to exploit successfully enough to reproduce. Note that the niche has now become a species-specific notion. The Eltonian idea of the niche as a role in the community was pretty much lost. As a result, another of my objectives in presenting the guild concept was to correct this confusing situation in which two fundamentally different ideas had the same name, and to give a new name to one of them. Therefore, the guild is now somewhat synonymous with the original Eltonian concept of the niche.

The species is a fundamental unit in nature, and the corresponding functional expression of the species unit is the niche. In this scheme, the guild, in grouping together species having very similar niches, is analogous to the genus in a phylogenetic scheme.

Returning to the definition of the guild, note also that the concept is not bound to a particular community. It may occur in several systems and thus becomes a functional unit available for comparative analysis. For many questions, it is the most appropriate unit for subdividing the complexity of the community. Also, by restricting attention to the guild, one is dealing with a meaningful subset of species which all have similar resource needs and similar behavior. As a result, all the members of the guild can often be validly sampled with the same technique. It is much easier to devise a valid sampling scheme for a guild than for a whole community. From an operational standpoint in community analysis, the guild is often the most suitable unit to use.

Other implications of the definition should be pointed out. Note that a species can belong to more than one guild, since it depends on the resource base that is selected for study. For example, a bird could belong to the foliage-gleaning, insect-eating guild if you are partitioning the community on the basis of food requirements. It could also belong to the cavity-nesting guild if you are partitioning the system on the basis of nest site requirements.

Finally, I feel it is important to always keep in mind that the guild concept might not have an objective reality in nature. In fact, one of the

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wonderful things about ecology is that there are few clearly defined
boundaries. It is probably impossible to draw up a set of standard rules for
how a community should be partitioned into the guilds, because it is not clear
that guilds are natural units corresponding to distinct groups in nature. I
am making a plea to keep the idea a little flexible because the quickest way
to destroy a useful concept in ecology is to lose sight of its intended
function or to impose a formality that does not exist in nature. Our concepts
must evolve as our understanding does. After all, the gene concept, which is
the central subject for many of the most reductionist biologists, has evolved
as genetic insight has grown.

In summary, the guild is a useful concept for examining questions that
concern species packing, interspecific competition, and convergent evolution
in different systems. It should also be very useful in understanding the
relative significance of functional roles in different communities and in our
generalizations about impact.

NICHE THEORY AND ITS USE IN THE ANALYSIS OF ECOLOGICAL SYSTEMS

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Introduction

The ecological community can be defined as coexisting populations of species in a given local area, such as a field, a wood, a pond, a section of stream, or a rotting log. It is understood that the scale of the community is such that all species come within the ambit of the other; species overlap in space if space is defined in terms of local habitats.

The null hypothesis in community ecology states that the presence and absence of species, relative abundance of species, and the kinds of species in a community are influenced only by the individualistic response of individuals in each species to the resources and environment in the area. No interactions between species within trophic levels play a role in modifying presence-absence, relative abundance, or kinds of species. The community is a simple sum of its parts. These conditions persist in ecological time and in evolutionary time.

Remarkably, the null hypothesis has been seldom stated, and less frequently tested, although the individualistic concept of species association was first proposed by Gleason (1926) and Ramensky (1926) more than 50 years ago. It should remain the basis for all studies of real communities, and new hypotheses should be erected only when direct evidence, based on detailed observation and experimentation, demonstrates that the null hypothesis is inadequate (Connell 1980). Mechanisms in community organization must not be invoked without direct tests to demonstrate the existence of such mechanisms.

Niche Theory

Niche theory and the guild concept help us to focus on approaches to community analysis, and the species on which critical tests for interaction should be made. In applying niche theory to the real world of field biology, Hutchinson's (1957) definition of the niche is most easily translated into practical use. According to Hutchinson, the **fundamental ecological niche** of a species is "an n-dimensional hypervolume . . . . . . , every point in which corresponds to a state of the environment which would permit the species . . . . . . to exist indefinitely." In practice, then, appropriate dimensions of the niche need to be defined and the distribution of species on these dimensions recorded. Whittaker, et al. (1973), extended the definition of the niche by using Hutchinson's definition to define the niche hypervolume of the species. Then the species population response within this niche hypervolume describes its ecological niche. Therefore, using one gradient of resources, such as temperature, Hutchinson's definition would simply define the limits of temperature tolerance of the species (Figure 1a), whereas the definition by

Whittaker, et al., would also plot the population distribution on this gradient (Figure 1b).

To measure this distribution in the field, a resource must be divided into subunits - the **Resource Set** is divided into **Resource Units** - and densities of organisms measured in each unit. A resource set could include such gradients as moisture, or host density for parasitic organisms. Then the following three steps can be followed.

Step 1. Estimation of Niche Breadth

The **niche breadth** of the species on the gradient of the resource set can be estimated using Levins' (1968) formula

$$B = 1 / \Sigma p_i^2 \ (S) \tag{1}$$

where P_i is the proportion of a species found in the ith unit of a resource set, S is the total units on each resource set, and B_{max} is 1.0 and B_{min} is $1/S$.

These estimates can be scaled to vary between 1.0 and zero by the formula (e.g., Fager 1972)

$$\text{Scaled } B = \frac{B_{calc} - B_{min}}{B_{max} - B_{min}} \tag{2}$$

Niche breadths can be calculated on several gradients to define the whole niche of the species.

Step 2. Estimation of Niche Overlap

When niche breadths on gradients have been calculated, the next step is to measure how much they are likely to interact with other species. Here the guild concept is applied because as Root (1967) emphasized, "species that exploit the same class of environmental resources in a similar way" will overlap significantly in their niche requirements.

Therefore, other members of the guild have niche breadths calculated on gradients, and then **niche overlap** values between species can be calculated using the formula of Levins (1968):

$$\alpha_{ij} = h \sum_{h=1}^{n} P_{ih} P_{jh} \ (B_i) \tag{3}$$

where α_{ij} is the niche overlap of species i over species j, P_{ih} and P_{jh} are the proportion of each species in the hth unit of a resource set, and B_i is the niche breadth of species i. The formula calculates an estimate of how one species may impact another species based purely on proportional overlap of each species and the niche breadth of a species (Figure 2).

In Figure 2, according to formula 3, species A overlaps species B more than species B overlaps species A; hence, the use of the B_i term.

Proportional similarity (PS) may also be used to measure overlap between species (e.g., Price 1971):

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$$PS = \sum_{i = 1}^{n} P_{mi} \qquad [4]$$

where P_{mi} is the proportion of the less abundant species of a pair in the ith unit of a resource set with n units. In the figure, PS would equal 0.17 + 0.17 or 0.34.

To calculate overall overlap, the products of the α values (formula 3) or PS values (formula 4) on each gradient of resources are obtained (Figure 3). These overall overlap measures indicate the species with the most similar ecologies and niche exploitation patterns, and those in need of most careful study. This study is undertaken in Step 3.

Step 3. Experiments on Interaction

We cannot assume, as Levins (1968) did, that α values or PS values provide an estimate of the force of interaction between species. We have measured simple overlap on gradients. Force of interaction must be measured with experiments. Therefore, detailed experiments should be undertaken to see if competition is important between species that have significant overlaps.

Another problem is that when niche breadths of species are measured in the field, distributions may be influenced by other species. Therefore, experiments should be done to define if and how other species interact and modify the occupation of the fundamental niche of a species. How do other species change the niche of a species from the fundamental niche to the **realized niche**?

Using these methods, a quantitative picture can be obtained of the distribution of species in a guild and the extent to which they interact. Now I will discuss some examples in which analysis of guilds has been undertaken. I have selected studies on insects.

Guild Analysis

Example 1. A Guild of Parasitoid Wasps on Sawfly Cocoons

A group of six species of parasitoid wasp which all attack cocoons of the sawfly, Neodiprion swainei, form a guild of parasitoids (Price, 1971). Step 1, as above, was to study the distribution of these species on resource sets. Five such resource sets were judged to be very important in the ecology of these wasps that search among forest litter for the sawfly cocoons formed among the litter. The resource sets were divided into two variables within plots and three variables that changed between plots:

A. Within-plot resource sets.
    1. Litter moisture content - a moisture gradient
    2. Seasonal activity - a time gradient

B. Between-plot resource sets.
    3. Host density
    4. Host species
    5. Plant community

Number of individuals on these resources were estimated by setting out host cocoons each week to allow attack and then rearing the parasitoids out in an insectary. Although resource sets 4 and 5 cannot be ordered, as on a gradient, each host species and plant community can be treated as a resource unit, and formulae can be applied to these data sets as to those on gradients. These data enable calculation of niche breadth for each species on each resource set.

Step 2 entailed calculation of proportional similarity between species on each resource set, and identified two species as the ecologically most similar species: Pleolophus basizonus and Pleolophus indistinctus.

Step 3 employed competition experiments between these species. When both species were placed in a single host cocoon, P. basizonus won in competition 68 percent of the time. In the field, P. indistinctus was displaced to the perimeter of the host population because of this competition and because it was univoltine and could not respond rapidly to rapid inreases in host density (Price, 1970). The better competitor, P. basizonus, was bivoltine and became most abundant when hosts were most dense.

In this study, guild structuring and the mechanisms involved were identified (Price, 1970, 1971, 1972, 1973). The distribution, relative abundance, and kinds of species that could live together were identified.

Example 2. A Guild of Leafhoppers on Sycamore Leaves

Eight species of leafhoppers in the genus Erythroneura live on American sycamore leaves (McClure and Price, 1975, 1976). These feed and breed on the leaves.

Step 1 involved a study of the distribution of the species on resource sets. These were divided into niche resource sets, or resources that varied within plots, or intracommunity factors, and habitat resource sets, or between plot factors, or intercommunity effect.

A. Niche resource sets.
1. Temporal utilization.
2. Distribution within the canopy.
3. Occurrence on leaves of different sizes.
4. Occurrence on leaves of different ages.
5. Location of feeding sites on the leaf.

B. Habitat resource sets.
6. Occurrence on trees along a moisture gradient from riverside up a slope away from the river.
7. Latitudinal distribution of species with respect to that of sycamore.
8. Distribution within a geographical locality.

Step 2 involved calculation of proportional similarity between all guild members. This showed that only habitat factors 7 and 8 were sufficiently different to permit coexistence of the species. Latitudinal distributions were most dissimilar with each species showing peak abundance at a different latitude.

Step 3 demonstrated experimentally that competition was very important in the guild (McClure and Price, 1975). The experiments involved pairwise combinations of species caged on individual sycamore leaves at different densities.

Much of the guild structure for these closely related species was identified by these methods.

Example 3. A Guild of Stem-boring Insects in Prairie Plants

Thirteen species of herbivorous stem-boring insects inhabit herbaceous plants in climax prairie communities in Illinois (Rathcke, 1976a, b). Step 1 studied the distribution of species on within-plot, or niche resource sets:
1. Plant species utilized.
2. Stem size.
3. Location within the stem.
Stems were opened and locations of species were recorded.

Step 2 again involved calculation of proportional similarity to estimate species overlap. Overlap was very high in this guild. Nine species showed more than 70 percent overlap on the plant species resource set. Mean overlap on stem size was 70 percent for species that shared plant species in 1970 and 41 percent in 1971. Mean overlap on location within the stem was also large, at 74 percent, for species that shared plant species.

Step 3. Rathcke did not do experiments, but she measured the amount of resource utilized by the herbivores. This was easily done, since each individual leaves a mine in the stem, showing tissues consumed as the larva feeds. Average utilization of a stem was usually very low; usually less than 10 percent of available resources. A single stem could support several larvae and tunnels seldom met, and dead larvae were seldom found within stems (Rathcke, 1976 b). Food and space within stems were seldom limiting. Species colonized stems in a way best simulated by independent attack by each species unmodified by the presence of other species. The niches measured in the field were fundamental ecological niches.

Therefore, Rathcke argued that broad overlap of species did not reflect strong interaction. Values of α (equation 3) provide no index of the force of competition. Such broad overlaps were possible because species interacted so little. Competition was very rare in the present and in the past so that niche segregation of species on the relevant gradients has not occurred.

The important point of this study for understanding guild structure is that stages 1 and 2 are merely descriptive and do not provide understanding of the mechanisms defining guild structure. Step 3 is an essential part of a study wishing to understand how guild members interact.

In these three examples I think the guild concept has been applied accurately and in the sense that Root (1967) originally defined. The two examples that follow are interesting studies, but use the guild concept in a less rigorous way.

Example 4. Guilds of Arthropods on Trees

Samples of arthropods were taken from tree species by spraying the insecticide pyrethrum into the tree and collecting fallen arthropods on a 1-m^2 sheet under the tree (Moran and Southwood, 1982). Three or four trees per tree species were sampled with five sheets placed under each tree. Specimens were sorted into species and guilds and seven guilds were recognized.

1. Phytophages – chewers, sap suckers
2. The epiphyte fauna – grazers on particles on leaves and branches
3. The scavenging fauna – feeding on dead wood and fungi
4. Predators – insect predators and other predators
5. Parasitoids
6. Ants
7. Tourists – species with no intimate association with trees but may use trees as shelter, or for sexual display.

This classification is not an appropriate use of the guild concept. Phytophagous chewers and sap suckers are not exploiting a resource in a similar manner. Root (1973) explicity divides chewers from sap feeders. Parasitoids, which are relatively specialized, are not all exploiting the same resources. Ants are important predators and may well be placed in the guild of predators, although they may be regarded as exploiting prey in a different way from nonsocial predators.

The authors then compared family composition in guilds, the similarity between guilds on different tree species, and the number of species, individuals, and biomass of arthropods in each tree species. However, such crude definition of the guilds fails to exploit the most useful application of the guild concept--that which identifies groups of species that are similar enough in their ecology to have the potential for strong interaction.

Example 5. Plant Defense Guilds

Atsatt and O'Dowd (1976) defined "guilds" of plants that have an influence on the plants with which they are associated. The guilds were regarded as "antiherbivore resources" in terms of the following:

1. Acting as <u>insectary</u> <u>plants</u> that maintain predators and parasitoids of herbivores on the associated plant.

2. Acting as <u>repellent</u> <u>plants</u>, causing difficulty for herbivores in locating associated host plants and causing early departure from host plants, if discovered.

3. Acting as attractant <u>decoy</u> <u>plants</u> resulting in more herbivores on the decoy than on the associated host.

4. Acting as <u>gene</u> <u>conservation</u> guilds, which may include any of the above guilds, where presence of guild members confers plant heterogeneity in the associated plant population in relation to herbivores. Such heterogeneity is difficult for herbivores to exploit effectively, and a diversity of plant genotypes is conserved under these conditions.

There is nothing wrong with emphasizing the importance of associated plants in communities. In fact, the ideas expressed in the paper are extremely interesting and widely cited. However, the use of the term guild is inappropriate for several reasons.

1. Guild members function as antiherbivore resources (Atsatt and O'Dowd, 1967). The term "resources" is usually used to denote essential aspects of the organism's ecology: food, space, time, breeding sites, etc. The plant does not exploit guild members; it merely benefits from their association. Therefore, the term "resources" seems inappropriate here, as is the term "guild."

2. In the same quote, we see guilds defined as resources, and yet Root (1967) defined guilds as groups of organisms that exploit resources. Thus, the function of the guild has been changed from Root's definition.

3. The use of the term "guild" by Atsatt and O'Dowd is more akin to its original use in the ecological literature by Schimper (1903), who used the term for the guilds of lianas, epiphytes, saprophytes, and parasites--all plants that are dependent upon other plants. Root (1967) pointed out that this usage has not been adopted in the ecological literature and that his definition uses the term in a new sense. It therefore seems inappropriate to resurrect Schimper's usage, and inaccurate to use Root's usage for plants that benefit associated plants in the ways defined by Atsatt and O'Dowd.

4. There is no emphasis on competition between members of a plant defense guild. And yet the guild concept was erected explicitly to enable more critical examination of competitive relationships, since guild members would be more likely to compete with each other than with members from other guilds.

Conclusions

The guild concept has been explicitly defined and rigorously interpreted in many studies. It will only confuse the issue to use the term in other ways. When departures from the strict usage are desirable, as will frequently be the case, then new terms and new concepts should be formulated. This will make ecology a richer science and a less muddled science.

Niche analysis provides a formal approach to the quantitative study of guild structure, dynamics, and the mechanisms resulting in structure. Basic studies have emphasized the study of interactive mechanisms within guilds, using the guild as the largest unit in the community for study. This emphasis was inherent in the original conceptual development (Root, 1967), and niche analysis is directly applicable. When the guild is used as the smallest unit of study, as in its many applications in habitat assessment, environmental impact assessment, and wildlife studies, it should be recognized that the concept was not originally developed for this purpose and may not be directly applicable.

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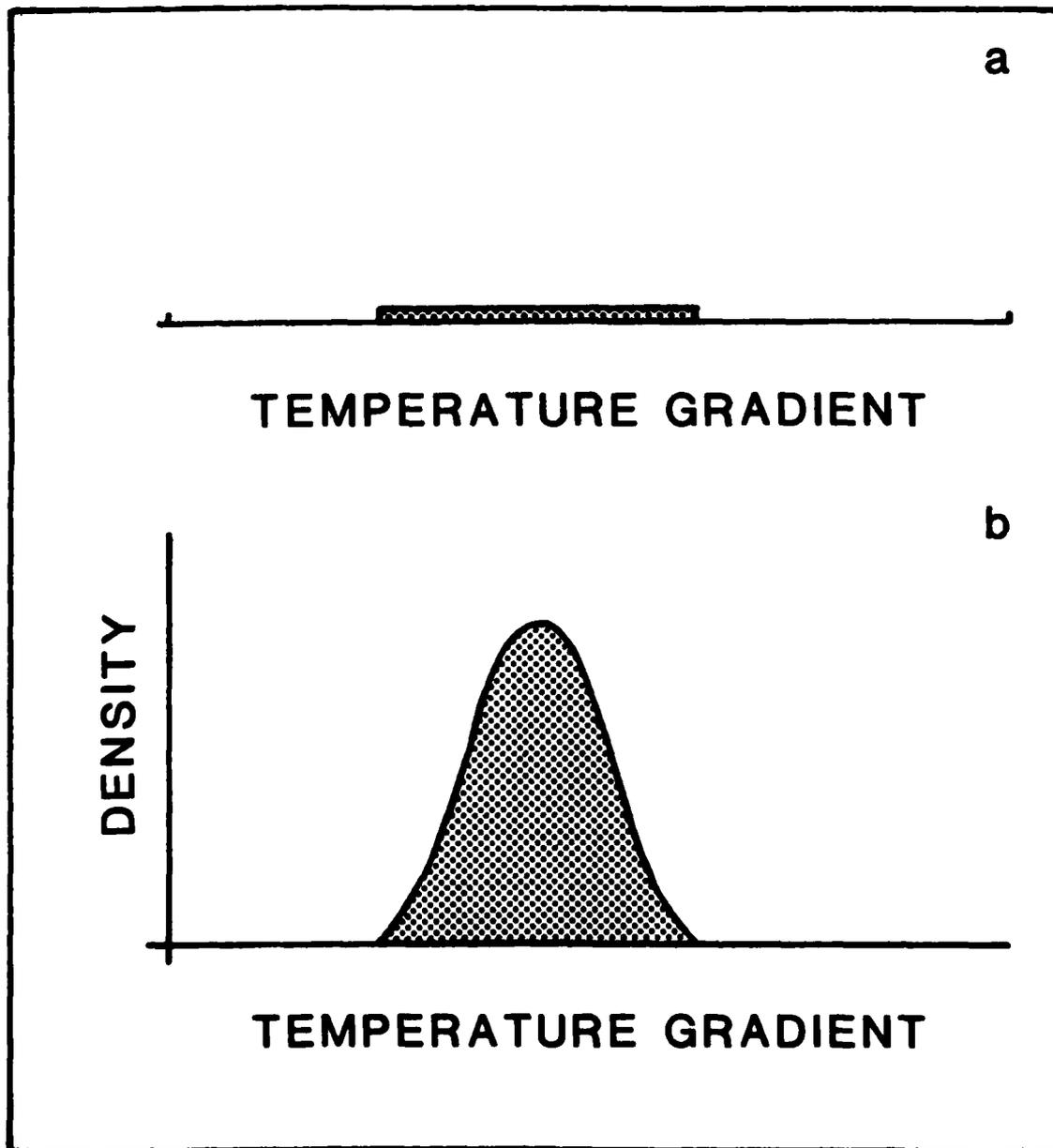
Figure 1. The temperature gradient niche dimension in relation to (a) Hutchinson's (1957) definition, (b) the definition by Whittaker, et al. (1973).
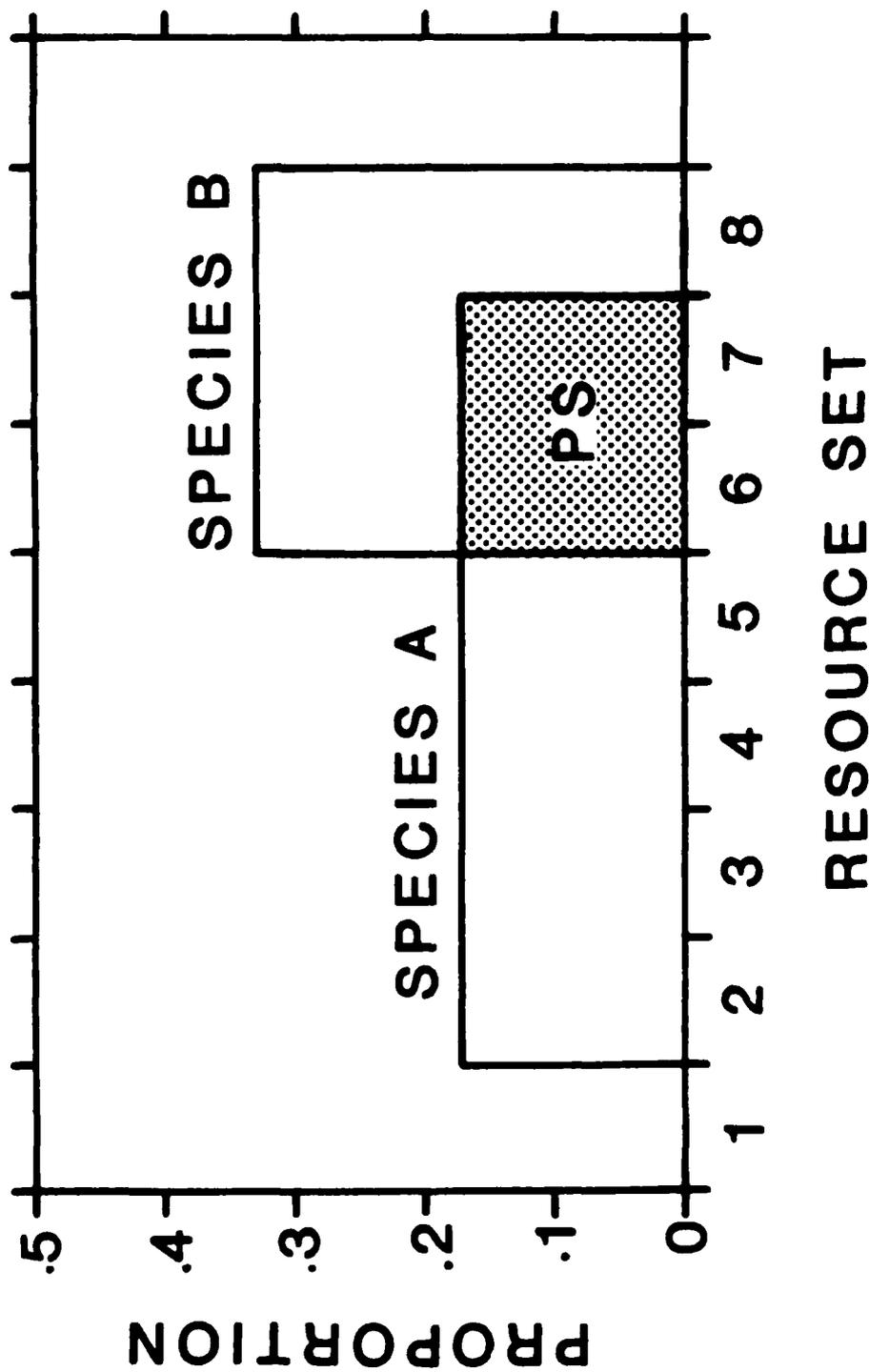
Figure 2. The distribution of two species on a resource set with eight units showing the proportional similarity (PS, shaded) between the species, and the form of the data necessary to calculate niche overlap values.

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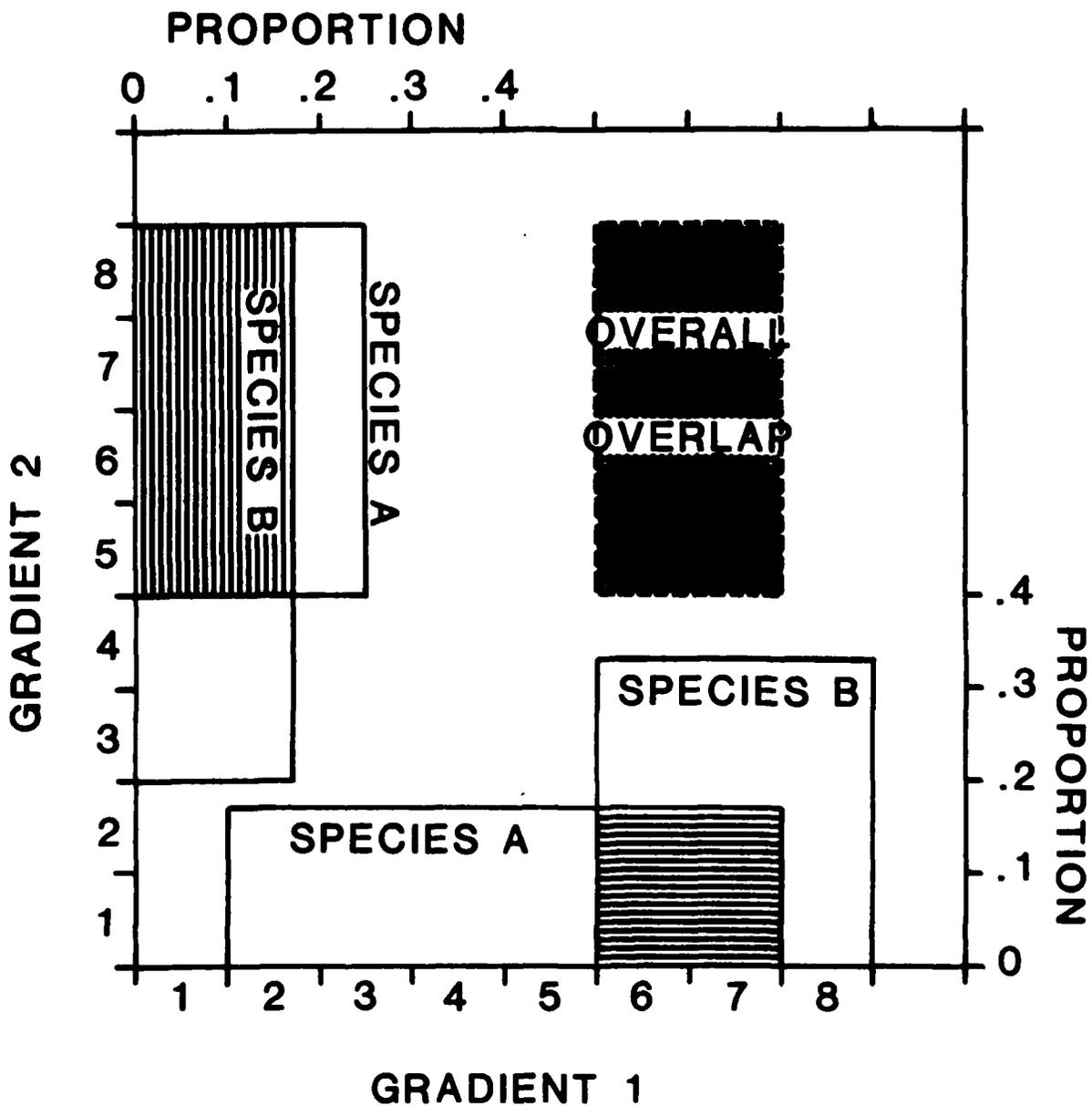
Figure 3. The proportional similarity of two species on two gradients showing the overall similarity on two niche dimensions, defining the area in which the species A and B overlap.

LIZARD AND BIRD GUILDS AND THE "JACK-OF-ALL-TRADES" PRINCIPLE

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In this presentation, I will be discussing factors which affect the species composition of communities. If one is going to study communities to figure out their origins, the factors that control the types of species inhabiting these communities and how they interact, or what happens if you change these communities, similar types of information are needed. For example, to understand how birds fit into these communities, one is not only interested in guilds, but how those guilds interact.

The guild concept is a useful technique for looking at the kinds of species in the community and getting some idea about how they interact. This requires a great deal of information. One good source of information is comparative studies. You would like to know what happens if the community changes in structure, if some of the trees are lost, or the vegetation changes. You would like to know what happens if you make the woods smaller instead of larger, or if you change the relative proportions of different types of habitat patches, such as fields, versus the actual patches of woods or shrubs. A number of situations can show where this type of occurrence takes place and many natural experiments can be compared. A study by Ned Johnson of boreal forest islands in the Great Basin looked at the sizes of bird communities and compared their compositions. What Johnson found, not too surprisingly, is that smaller islands have fewer species. But if he had grouped them into functional guilds and then compared them among the large and small islands, he would have found that the guild number does not change much. Most of the guilds present on large islands also occur on the small islands. What happens is that the number of species in the guild drops. In the small islands you may find only one or two species in each guild.

This type of pattern has also been found in other types of studies. Bob Howe at the University of Wisconsin has completed two studies that compare bird species breeding on islands in Minnesota lakes with those found in Wisconsin woodlots of different sizes in order to see what species are present. He noted that not only does the number of species drop off, as expected, but predictable sets of species can be found in the smaller patches.

I would like to approach this subject by using another model that is ideal for approaching some ecological questions. Then I will try to convince you that it has a lot to tell us about birds.

Anolis lizards are primarily tropical, although at least one species is very common in the United States--the so-called American Chameleon, Anolis carolinensis. Within this one genus, all individuals are very similar in form. This will give us some idea of how a generalized animal can be used to answer questions dealing with birds or other animal communities.

In comparison to other types of lizards, anolis lizards are peculiar. They are not like the desert type of lizard and are similar to birds in many ways. In terms of their biological characteristics, they vary considerably in size, and some can change color dramatically. The males have a dewlap which

they use essentially to advertise territory, display against trespassing males, and attract females. Both the dewlap color and the color of the body patterns are important for communication within or between species. They are fairly generalized insectivores; their mouth size indicates that they eat insects of sizes similar to those eaten by many insectivorous, foliage-gleaning birds. They have very large eyes and are diurnal; the species which have been studied seem to have color vision. Thus, they hunt in patterns similar to those of birds, are arboreal, and hunt over all types of surfaces, from large trunks to small twigs. The small pads and sharp claws on their feet allow them to climb vertical surfaces. Most of the species spend the majority of their time above the ground. Thus, this group of organisms, despite the fact that individuals do not have feathers and are poikilotherms, is a generalized insectivore, mimicking many aspects of insect-eating birds. Since they do not fly, they are much more tightly constrained to vegetation, thereby giving us a clear look at how they are tied into vegetation.

These lizards are found in the West Indies, which offers many advantages such as many patches of different sizes. There are more than 100 species of Anolis lizards in the West Indies. Since they are the dominant foliage insectivore and cover a range of islands of different sizes and habitats, they offer a large set of natural experiments. The large islands (the Greater Antilles) all have a large number of species, with 40 species inhabiting Espanola. There are probably many more than 40 species on Cuba, 7 on Jamaica, and 11 on Puerto Rico; in given habitats on these islands, several species may be noted living in the same spot.

Examination of the species on the large islands shows that they consistently differ in a number of ways, so that on a given island, species will be found occupying different portions of the vegetation. Ernest Williams and his associates (Rand and Williams, 1969; Williams, 1972) called them ecomorphs. They are forms which differ in their color, behavior patterns, and morphology, and are bound to certain portions of the habitat. One can find giant forms in the canopy (the so-called trunk crown form which exists over the tree trunks up into the crowns of trees), forms on the trunk, forms that stay near the ground on large surfaces like the trunk, forms that are on bushes and grass (sometimes separate), and twig forms. Even though anoles of Jamaica are not closely related to those on Puerto Rico, many forms can be found that can easily be classified into one or another of these categories. Thus, they have communities that are quite unstructured among the various locations, even though the anoles in the varying spots are not that closely related; this suggests that the habitat strongly influences the types of lizards that are present.

Let me give you an idea of some of these forms. There is a giant form (Anolis equestris) in south Florida and the American chameleon (Anolis carolinensis) that generally changes color, and is a trunk crown form. There is a trunk form with very special adaptations for running rapidly up and down wide surfaces. This form is also found on rocks and sides of houses. There is a trunk ground form found near the ground which frequently hunts sitting on a tree, looking down at areas around the roots and out on the ground for food. The very small grass bush form has long legs, does a lot of jumping, and lives in the jumble of herbs and small bushes near the ground. There is also a twig form which is very small. The rock form, which exists on the small jumble of rocks occurring in certain portions of central parts of Cuba and Espanola, is also very small--only an inch or two long.

There is an incredible diversity of species on these islands. In terms
of guild theory, they could all be termed as belonging to one guild in the
sense that they are all arboreal insectivores. All are fairly general in the
types of insects on which they feed. About 10 years ago, when I was writing
on this subject, I asked Dick Root whether I should call them one guild, and
he explained that it just matters what question you are asking. They are all
very similar in the broad sense that they exist over a wide spread of
vegetation; however, within that group there are particular types, such as the
ecomorphs, and from island to island, the ecomorphs are in the same type.
Only one individual of each ecomorphs tends to be found in one spot. For this
purpose, I will call them all guilds, and within that guild, talk about what
types of factors set up and why different species are lost from one spot to
another. Returning to the subject of the boreal forest "islands," species
within guilds decrease in moving from large islands to small islands. The
same thing happens in moving from large to small islands in the West Indies.
Is there some predictability to that pattern? Can those lizards be observed
and studied to find out which species are likely to be lost? Does it follow a
common pattern? I would like to give you some idea of how they are tied to
the environment, and then show the kinds of situations produced when the
environment is modified. The principal study located in southwest Haiti had a
variety of habitat types. In some remote portions there are still some
forests available, although most of it has been high-graded. Habitats exist
in this small range. However, in studying the seven species present and
watching where they exist in the vegetation, a height separation is noted.
Examination of the vertical occurrence of lizards shows that there are only a
few species very high in the canopy; most of them exist lower down.

Looking more functionally at the lizards, they exist on branches, leaves,
or trunks of various types, which differ considerably in diameter. Their
ability to exist or to move and operate on surfaces of different diameters is
similar to that of many animals. Looking at the types of diameters they
occupy, going from very small diameters (3 mm) to larger sizes (up to 1 inch),
one finds that the species separate into groups or types that occupy large
surfaces or very small surfaces. It is not a linear relationship, since most
of the species group at the small end. To use a human analogy, walking on a
sidewalk does not require much coordination, but walking on progressively
narrower surfaces becomes more and more difficult; the same is true for
lizards. Thus, operating on very small perches is very difficult for them,
and this ability to use the surfaces is where the primary separations occur.

Most of our studies on anolis lizards deal with how they use surfaces.
The lizards must not only operate on the surfaces, but also be able to search
along or between these surfaces. To do this, they must either move along the
surface or jump to another surface. Comparing the types of function in terms
of the lizards' morphology shows that some types will move along surfaces.
Those on wide surfaces can move rapidly, while those on small surfaces are
tightly constrained. Many of them crawl, while many others jump frequently
from surface to surface. If the surfaces are close together, the lizards will
jump; those that live in areas like the canopy, where surfaces may not be
close together, are better adapted for crawling. Functionally, one can find
types that are adapted for crawling on narrow surfaces, types that are adapted
for jumping between clusters of small surfaces, and types adapted for running
on large surfaces. The morphology of the lizards actually goes along with
those differences.

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In trying to decide what this means in terms of habitat, one finds that different clusters or types of surfaces are available in habitat. If you can think of them as "jungle gyms" in which there are collections of large surfaces such as trunks, those adapted to large surfaces can run over the entire length, from the ground up into the very high areas. One type of lizard that occurred over a high vertical range was adapted to wide surfaces and could go from near the ground all the way up the wide surfaces, wherever they occurred. Others are adapted to widely separated narrow surfaces like the canopy and crawl back and forth from branch to branch. Others which are down further where the surfaces are small but very tightly packed jump from surface to surface.

Essentially, the ecomorph types can be fit into specific portions of the habitat. Those that are in tight little clusters of grass-herb areas do a lot of jumping; most of their movement from spot to spot is primarily by jumping. Both small individuals in bushes and large individuals in the canopy do a lot of crawling. Those at the bottom exist on the large surfaces and move primarily by running. The morphology goes along with this in terms of leg proportions and other items that can be measured easily. If these variables are put in the habitat, it is found that in the progression from very low, shrubby-type areas up into the forest and finally into the canopy, both the horizontal distribution of the lizards along the ground and vertical distribution tend to follow the type of habitat that they use. Thus, lizards like Anolis carolinensis that crawl in widely separated narrow perches can do the same thing in the canopy, regardless of the canopy's location. The portion of the habitat that they can use is determined by their morphology and by where the type of microhabitat they use occurs. Lizards that use wide surfaces well have morphology that makes it difficult for them to either crawl or jump; those that crawl are not very good at jumping.

This introduces the "jack-of-all-trades" principle: that for any one of these things, it is difficult to do all of them well. There are a number of specialists at one skill, and being a specialist at one skill precludes being a specialist at a second skill. It's not just a matter of broad or narrow niches, but where your niche is. Animals on wide surfaces may actually have fairly tight requirements, but one that occupies a wide surface has a lot of surface available and could therefore exist over a wide area. A lizard which specializes in the grass-herb type of area exists in fields or spots where that habitat is developed. This species cannot survive in a more sparse forest understory. Thus, where a species can exist depends on what its specialty is; where there is enough of each type of habitat, all species will be observed.

In the spot I studied in Haiti, there were seven species in one area. The important thing then is to look at where they are on surfaces, and if we compare the species over the range of surfaces, we can envision what I call an "adaptive circle," and show that those that like the trunk have a wide range of vegetation types to occupy. Others, such as grass types, have a very narrow range. The question is, if you change these habitats, what kind of species would you expect to find there? Or one could ask, if you took all the species out and put one back, where would you expect it to end up? And one might expect a single species to be somewhat like A. coelestinus whose morphology allows it to use a wide range of the habitat. What is observed is that where A. coelestinus occurs with grass species, it does not use the grass

well and tends to be excluded from the grass. Here at least competition is likely to be implicated. However, in habitats where the grass species does not occur, A. coelestinus (particularly young individuals) uses this area and fills in that spot. Anolis coelestinus fits into what we might call a generalist, or "jack of several trades." It's able to do lots of things but none of them particularly well, where there are specialists using lots of the other spots. Anolis coelestinus tends to be a good colonist, moving into new habitats and into small islands. Anolis Carolinensis, the American chameleon, is very much like A. coelestinus; it has occupied most of the small islands through the West Indies and has invaded North America.

On small islands that were colonized very early, the set of species seems to be very constrained. Only one or two species are present on the Lesser Antilles. In studying the patterns of body size in these islands, Tom Schoener (1971a, 1971b, and Gorman 1968), found that where two species occur, one is large and one is small, and where only one occurs, it is intermediate in size between them. However, we find that the large one is very large, and that the small one is large relative to those on the main island, and is very much like A. coelestinus. Further examination of these islands indicates that those in the southern part of the Lesser Antilles were probably invaded from South America. For example, two species occupy Grenada, and they would be expected to look like a trunk crown animal. However, comparison of leg length to body length showed a separation between the two. Their behavior (i.e., the way they use the vegetation) also separates them. The one with smaller legs does more crawling, while the one with larger legs does more jumping.

A look at the northern end of the Lesser Antilles (St. Kitts), shows that another two species occupy a similar area of the habitats. They also have a similar size range--a large one and a small one, although the small one is smaller than would be expected. The large one looks sort of like a trunk crown animal and has a similar range of habitats. In this case, the small one looks a little different; it's more like a trunk ground animal, even though it is small. It occupies a wide range of habitat, but does not separate as well from the large one here as on Grenada. A look at the morphology provides some idea of the problem. In this case, the small species overlaps the smaller individuals of the large species. The morphology is very similar, and the behavior of the small members of the large species is very similar to that of the small species as a whole. The distributions and the habitats suggest that there is a great deal of competition. In looking at how they use the habitat, one finds that, on the average, the large species can move into more types of habitats than the small one, even though their morphologies are similar. Comparing the percentage of different types of perch diameters used in the habitat shows that the small one uses primarily small-diameter perches, and that the large one uses larger diameters but also includes small diameters. If the large species are separated into adults and juveniles, the juveniles' pattern is very similar to that of the small species.

At St. Kitts, there is a large difference in the vegetation, which is very rich, and there is a great deal of difference in the types of perches available, so the species can be separated. The same pair of lizards can be compared in Antigua, where the vegetation is much more impoverished, and where its structure is essentially changed. Here, although the ability to separate the habitat is much smaller, there is still a similar pair of lizards to work with. If one observes how they separate by perch size, not as much separation

is found. The large species is still using more larger-diameter perches, and
the small one still heavily uses the small-diameter perches; however, in this
case, there simply aren't many large-diameter perches available. Comparison
of these species shows that their behavior is rather different. The large
species has shifted morphologically from the small one. This is an example of
a case where moving from a habitat where the species separate by habitat
differences into a situation where the habitat differences are not as great
and the species are shifting more morphologically suggests that the
morphological differences are important to defining their co-existence. The
important thing is whether the shifts happen rapidly. If these types of
vegetation shifts, such as the loss of forest, occur rapidly, instead of
happening gradually over centuries, two species will be forced into
competition, and one very likely could not survive or would be less likely to
survive over the short term. However, if the changes happen over a very long
time, morphological adaptations can occur. In looking at similar patterns on
lowland Haiti, one finds that in heavily modified areas, the specialists tend
to be lost, leaving the generalists.

     If the habitat is modified by cutting down the smaller patches, the
specialists will drop out and the generalists will tend to survive. If the
specialists survive, it is only ones that are particularly adept within the
habitat. For example, species such as grass anoles may survive in these
patches, but they are still patchy and in most cases, a generalist that uses a
wider range of habitat will be observed.

     The important reason for observing these examples is that by taking a
functional look at the way a guild uses the habitat, one can identify which
species are the generalists and which ones are the specialists. By looking at
the portion of the habitat they use, the ones likely to survive in altered
habitats can be predicted. One can also look at these examples functionally,
beyond the taxonomic group, and compare their foraging with that of birds
found in the canopy, where there are relatively few anoles. The birds which
occupy the canopy in the West Indies tend to be migrant warblers, which can
easily fly after food items. They can easily move from perch to perch in ways
that the lizards cannot and therefore forage better in the canopy. As a
result, there are fewer lizards in the canopy; however, in the lower areas on
the island, the lizards can move more easily from surface to surface, run over
surfaces, and jump among closely spaced stems. Likewise, in the lower areas
of the West Indies, relatively few foliage-gleaning birds are noted. Thus, by
functionally looking at how they are using the vegetation and at their
activities, one can make comparisons across taxonomic boundaries.

     For another comparison, in looking at birds at various locations in the
forest, one does not frequently find the types of tight coupling of one type
of species in a spot that are found with the anolis lizards. Also, the birds
are not as tightly coupled to the habitat as the lizards, since they can fly;
however, they must still deal with moving on these surfaces. A black and
white warbler can move on thin twigs or on trunks. The types of adaptations
required to move from spot to spot and from surface to surface are still
important, and even though one bird has a range of abilities, it can still do
one thing better than others. If one observes how birds use different sources
and observes their ability to use different types of surfaces to hunt for
these resources, differences similar to those found in anolis lizards will be
noted, and a series of generalists and specialists will be found. One could

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then predict that changing situations and moving from large to smaller and smaller habitats will change the birds' composition. Particular species could be predicted to occupy smaller patches. Thus, looking at the various types of modifications and functional differences among the species within guilds, one cannot only predict what species will decrease, which is obvious, but also which species are likely to be lost. This information can be used to assess the types of changes being made in different areas.

STRUCTURE OF PLANT COMMUNITIES: STRATEGIES FOR THE
COLONIZATION OF DISTURBED AREAS

Julie S. Denslow, University of Wisconsin, Madison, WI

The guild has been defined as a group of organisms that use similar
resources in similar ways. I would like to set that against the competitive
exclusion principle, which states briefly that two species which depend on the
same resources at the same time cannot continue to coexist in the community.
The two are not unresolvable. The guild concept has been particularly
important in focusing our questions on which species we should examine to
better understand the organizing mechanisms of communities. Within guilds, we
would address questions, such as: what are the competitive interactions and
the trade-offs of adaptive syndromes that underlie the diversity of coexisting
species; and, what are the limits of similarity between existing species?

Traditionally, the guild concept has not been applied to plant
communities. There have been only three or four papers in the last 10 or 12
years in which the guild concept has been applied directly to plant
communities. This is at least partly caused by an historical difference in
the approach to the study of community structure. The plant ecologists have
tended to examine vegetation as a unit and to study variation, abundances,
composition, and structure of communities as a unit, while animal ecologists
have tended, at least historically, to look at population interactions. Also
contributing to this lack of application of guild and niche concepts to plant
communities is the difficulty in imagining how co-occurring plant species
could be partitioning a resource gradient. How could they possibly occupy
different niches when their demands on the resources are so similar? Plant
species essentially all require light, moisture, and inorganic nutrients. How
can these sorts of requirements be subdivided sufficiently finely to permit
coexistence or to promote our application of competitive exclusion principles,
Hutchinsonian niches, coexistence, and so forth?

We have boggled both at the ability to describe different niches for
different species of coexisting plants and also in our failure to
conceptualize the kinds of mechanisms that might be involved in the
partitioning of these resources. I would suggest that the root of our problem
has lain in our propensity as plant ecologists to examine the distribution of
adult trees. This is typically the way plant ecologists get an idea about the
structure of the vegetation community and sort out the important interactions.

We measure basal diameters of trees and get a list of tree species and
perhaps special distributions, and try to relate their special distribution to
some kind of a habitat variation. Frequently, we find correlations between
the distribution of adult trees and components of the habitat, especially
things like soil drainage components, distribution over soil catenas, acid-
base differences, and rich top valley differences. These are very common
sorts of composition gradients defined in vegetation communities. But there
is still a very large residual diversity in a plant community that we are
unable to define by variation in soil composition. As in tropical botany, the
problem increases exponentially when we get into tropical species diversity
with the coexistence of several hundred species of trees. We can also look at

stratification of trees or vascular plants in a community and discuss partitioning of a light gradient from the forest floor to the forest canopy. But still we have difficulty in imagining how a plant species could sufficiently finely partition this gradient to account for this tremendous species diversity. So I would repeat that our problem has lain in the generation and distribution of adult species.

Where are the important interactions that are influencing the coexistence and the competitive interactions of plant species? Are they at the seed and the seedling level? When we begin to examine the interactions at this level, we begin to understand many more of the factors that are contributing to the composition of plant communities. Here, we are especially talking about two particular components of seeds and seedlings that contribute to these interactions. One is the ability or the probability of a seed occurring in a particular place at a particular time. This is basically the dispersal ability of seeds as a characteristic of an individual plant. Also, how well does a particular plant or a particular species disperse its seed? This refers not only to the range of the seed shadow and how far away the seeds get from the parent plant, but also the density of that seed shadow. The other component of the seed/seedling ecology is a seed's ability to germinate under particular microclimatic conditions and the probability of that seed establishing an independent growing seedling. Thus, we are examining two essentially quantitatively different responses of a plant to the problem of establishing its offspring in a particular environment, and we see that these two different requirements impose very different constraints on the seed structure. In this respect, then, the most important organizing principle of a plant community becomes those forces that create patches, gaps, or sites for the establishment of seeds—essentially, disturbances to the community.

The jargon does not provide an adequate word for the generation of these sites. We tend to use words like "disturbances" and "perturbations;" however, there is a very strong value component to these words, in that they tend to imply that this is an extraneous force on the community and perhaps something that should be avoided. This is not the case. Disturbance factors are as much a component of the community environment as rainfall, seasonal temperature regimes, soil patterns, and so forth. This is something we have to consider as part of the natural environment. Perhaps this is analogous to the soil structure, since disturbance factors cannot be considered in the absence of the community; this is because part of the components that contribute to the probability of, for instance, a tree going down will be the structure of the tree itself.

Whether gaps tend to form in a forest may be very closely related to the forest canopy structure. If a forest canopy is very uneven, gaps are much more likely to form than if the canopy surface is very smooth and tight. For instance, in a montane forest, in which there is a lot of wind pruning, the canopy surface will be very smooth, and there will be much less tendency for a tree to be caught by the wind and blown down than in a situation where the canopy is really uneven. Thus, these gap-forming processes are also tied very closely into the forest structure itself.

Another component might be rooting depth and soil depth as a contributing factor to the depth-forming processes in a community. A resource gradient varies in two or more important ways, one of which is the microenvironment

associated with the gap itself. We include in this resource gradient such components as the amount of light reaching the forest floor, the temperature, the relative humidity, and variations in soil characteristics. There are also variations in these environmental characteristics among gaps that have different origins. (For instance, a landslide versus a tree fall, in which a lot of litter is created.) There is a microenvironmental component and a distributional component associated with these gaps, as well as both spatial and temporal distribution. Some gap types may be very rare, and others may be very common.

Now I will contrast regeneration in different gap types so you can see how they might be used as a basis for recognizing different guilds within a plant community. In a forest community, we might recognize a gradient that is based simply on gap size as a very simple situation. If we look at a gap created by the fall of a single tree, the microclimatic condition on the forest floor where the seeds are germinating will be directly related to the size of that gap, because the amount of the sun's arch that is being intercepted (that is, the amount of direct sunlight falling on the forest floor) is a function of that opening. Those conditions for a small gap are going to be much different than for a large gap. Of course, this is a continuum, although there is some evidence that there are cutoff points for certain types of species.

The microclimatic conditions on the forest floor for small gaps are going to resemble understory conditions of the forest more closely, while the conditions in large gaps will resemble those in an old field, or be much more variable and much more extreme. Thus, we have gradients running from humid at the gap edge to dry in the center, and constant temperatures at the edge to variable in the center. Probably the most important component in the tropics is that the daytime temperatures tend to get very high and nighttime temperatures get very low, with the hot temperatures being especially critical. Certainly, the duration of full sunlight will be variable. The soil structure is much more likely to be intact in small gaps than in large gaps.

Another component of gap sizes will be their distribution in the forest. This component will vary, depending on the environment, the wind conditions, and gap-forming processes within a particular forest. In the forest in Costa Rica, smaller gaps tend to be very common, and large gaps are rare. These small gaps might be branch falls or single-tree fall gaps, while the large gaps are created by the fall of many trees. How then do we expect seed dispersal/establishment characteristics to interact within this resource gradient? Basically, the interaction is tied to trade-offs that are keyed to seed size itself. The plant species that establish seedlings in smaller gaps in the rain forest tend to be large-seeded, and those in the large gaps tend to be small-seeded. Those differences bring a whole sweep of associated ecological consequences. For instance, large seeds would tend to be poorly dispersed, simply because of animal disperse sanctions; fewer species carry a large seed than a small seed, so small seeds tend to be well dispersed. There is an energy trade-off, depending on whether a species produces very many small seeds or relatively fewer large seeds. This would also contribute to the dispersal efficiency of the plant species. Large seeds tend to produce large seedlings, which are more competitive upon germination and tend to be more shade-tolerant. As a species, the smaller plants also tend to be more

shade-tolerant, such that they will last for extended periods of time as a seedling rather than as a seed. In contrast, large-gap species tend to require a high amount of light so that there is no germination at all under low-light conditions. They require a relatively long duration of full sunlight, perhaps also related to the high temperature, for germination. The seedlings produced are very small, and there must be a great deal of light for them to grow. The large-gap species also make better use of the full sunlight. Under high-light conditions, they will grow faster, while small-gap species will not grow at all, and probably will not even germinate under the low-light conditions. Basically, there is a sweep of ecological characteristics of these plant species long associated with the terms "pioneer" species and "climax" species. I think this is a better way of looking at the situation, because it sets it within the overall context of the community. These different types of species all coexist within the community and are all equally valid members of the community and therefore must be considered when discussing management of the community as a whole. When we talk about "pioneer" and "climax" species, there is a value judgment placed on the quality of the species involved.

What happens when plants begin colonizing human disturbances? The area I will be talking about is in the northern part of Antioquia, Colombia. The site is at about 400 m elevation and is in the foothills of the Andes. I was essentially interested in the partitioning of a resource gradient which might be called a disturbance gradient, with certain reservations about use of the word "disturbance." I used the agricultural system to generate the resource gradient. The people in the humid tropics use a system of agriculture called slash and burn, shifting agriculture. The essential pattern is that the older forests are cut, and the slash is allowed to lie on the ground for varying amounts of time while it dries. The slash usually converts to ash, especially the smaller twigs and the leaf litter, and the crops are then planted among the branches. There is no cultivation, disturbance of the soil, or fertilizer, other than the ashes or insecticide. At one period part way through the maturation of the crop, weeds are cut with a machete. Because of the large amount of rainfall and the high temperatures in the tropics, the higher nutrient levels created by the ash are very quickly leached out of the soil. The soil fertility drops, the soil compacts, and weeds invade, with the result that the fields are abandoned after maybe one to three crops. The farmer then moves on and cuts another piece of forest. There are variations in the frequency with which these fields were cleared, resulting in a change in frequency and intensity of disturbance. This creates a disturbance gradient in which the composition and structural changes of these fields can be studied.

I essentially picked out three main field types. In one, the forest that was cut down was fairly old, probably more than 20 or 30 years old. Two plantings were made every year in this particular area. The first plantings were made during the dry season during which there was about a month in which the slash was dry enough to get a good burn-off. The second planting was made during the short dry season in August in which there was a slight drop in the amount of rain.

In the second type of field, there are not enough consecutive dry days for the slash to dry out, so it can never be burned, and the corn is planted among the litter. Because it is planted raw, the cleared vegetation is not as

high and dense or of much volume, so these fields are cleared about every 5 to 7 years. This is a much higher frequency of clearing, so the vegetation that is cleared is younger.

In the third type of field, vegetation is cleared annually, and the field is also grazed. There is no pasture improvement, such as seeding of pasture grasses or fertilization. Once a year, farmers cut down all of the woody growth and let it lie unburned on the ground. What is provided is a gradient of different rates and frequencies of disturbance intensities. A series of fields was chosen as replicants of these different field types, and the vegetation was sampled. The composition of vegetation was analyzed using polar ordination to find out whether disturbance was an important factor. Polar ordination is essentially a form of mapping procedure in which stands are compared on the basis of the species occurring in them and the relative abundance of those species. Basically, the results of the vegetation analyses should show the same disturbance gradient that was the basis of the fields' selection. The fields were selected on the basis of their histories, and the history was reflected in the vegetation's composition, which changes across a disturbance gradient. The succession rate also changes following a disturbance.

Permanent quadrants in each field were sampled at various times after the disturbance. The fields representing the forest-cleared stands essentially changed the most in composition over the 8 months of sampling. The pasture-cleared stands hardly changed at all, and the scrub-cleared stands changed somewhat intermediately. This suggested that there are different processes of dispersal and establishment that contribute to the differences in vegetation composition. Part of this is reflected by changes in diversity. There were not great differences in plant species diversity within the fields, but there were quite striking differences in how that diversity changed over time.

The most important factor is examining the change in diversity over time. Within the forest-cleared stands, diversity increased with time after disturbance. Diversity increased initially and then stabilized in the pasture-cleared stands. This suggests that the establishment processes within these fields were quite different. If we examine the composition of vegetation on a very general level of plant structure, we see that there are strong differences in the kinds of plants that establish in these different fields. Trees occur in the forest-cleared stands, but not in the pasture-cleared stands. Large herbs are found in the forest-cleared stands, but fewer are found in the pasture-cleared stands.

We also find that dispersal characteristics of the plants occurring in these fields are much different. The animal-dispersed species are the most efficient dispersal forms, while wind-dispersed or capsule-dispersed species are less efficient. We can also look at a series of plants occurring across this disturbance gradient and find that individual plant species tend to divide up the gradient.

In conclusion, I would like to emphasize the utility of looking at the structure of a community by using the characteristics of gaps or disturbances. The gaps create the resource gradient, which is partitioned and which forms the resource gradient on which the different guilds divide. This approach to plant community structure provides a much more powerful lever in

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predicting what kinds of effects different management practices might have on the community. Thus, we could say that the composition of a natural community is the result of a diversity of gap-forming processes and that the composition of the community reflects the prevalence of particular types of gap processes and gap types. If we change the composition of the gaps (for instance, if we create larger gaps by selective logging or if we prevent the formation of gaps by fire control in communities where fires are a common component), then we would expect the composition of the communities to change. We would also expect species that depend on those gap types to drop out. If we are interested in maintaining a high species diversity in the community or if we are interested in maintaining or revegetating communities on mine tailings, river edges, or places where the vegetation has been completely lost, we must do it with the continued existence of disturbance processes in mind.

Q. (Peter Landres): I wonder if you could comment on your original definition
of guilds, which talks of the criteria of behavioral similarity in light of
recent, more theoretical studies, and with your idea that you want to get out
of the taxonomic arena.

A. (Richard Root): I think there is a certain amount of unnecessary
quibbling, in that similar use, or manner of use, is not necessarily
restricted to a taxon. There is a certain amount of arbitrariness in what I
mean there, but certainly we see convergence in different taxa, for instance,
leaf mining. Many orders and many families of insects are exploiting the leaf
structure in what appears to be a similar fashion. But what you are asking
about is a much broader problem. It's a problem that we face at every level
in ecology, and it's a scaling problem. One cannot legislate common sense,
and in defining the guilds or whatever, I think we have to consider that the
central idea is to define the unit in a way so as to observe patterns, rather
than etching in marble what a guild is and quibbling about all of the
details. I kept it a little general. I think Peter Price brought up some
good points about places where the definition has just been carried to the
extreme, so that the original intent of the idea was lost. And I think that
is wrong. I would sort of say that the scaling is really a secondary problem
and that it is difficult to make a set of rules, although I can suggest some
boundary conditions around something like the guild concept. But the scaling
is a secondary problem. I think that we could take a note from taxonomy,
phylogenetic taxonomy, and the numerical taxonomy programs. We would probably
get a canned program from your local taxonomist, which would shake things out
in hierarchies or degrees of branching. There are very good programs for
denoting groups, and you could do it according to some mathematical rule. Now
as to which of these groups is a guild, component community, or whatever is
secondary, don't forget that the object of making classifications is to define
a unit that will reveal a significant pattern. Early in my talk I was talking
about the art. There is an art to ecology, and you can't substitute a bunch
of mumbo-jumbo for being an excellent naturalist. I think that is very
important. The guild idea was originally put forth to have something to do
with competitive interactions. It also had something to do with the adaptive
commitment of a way of life. And for those of you who are interested in
impacts and characterizing ecosystems, defining units so that it is
appropriate to your needs would be important. We can't go around making
generalizations about the effect of this impact on all of the species. One
would like a bigger generalization than that. Well, you can't go all the way
to trophic levels, because then you try to make a generalization about all
herbivores, for instance. Anyone who does that is just pulling your leg.
There is really a need to define units around which appropriate
generalizations can be made about the question. Some of those are guilds, and
some might be something else. I think that is the thing that the Corps and
others really have to keep foremost in their minds. Now with that in mind,

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*Only those questions and answers pertinent to the further understanding of
the guild concept and its applications are included.

here are some general rules for defining guilds. I said it is not possible to set standard rules for partitioning communities into guilds, because the boundaries selected will depend on the questions being addressed and the naturalist's sense of which are the most critical interesting source dimensions in a particular situation. The limits of what we can call a guild must be somewhat arbitrary, so the term should always be reserved for groups of species that: (1) are relatively close in being potential or actual competitors, and (2) have adapted to a common set of selective forces associated with a resource and the exploitation pattern that they share. In no case should the resource base on which a guild is defined be so broad as to make the term synonymous with another established concept, such as the trophic level.

SESSION II: GUILD APPLICATION TO CLASSICAL MANAGEMENT

INTRODUCTION

Timothy C. Moermond, University of Wisconsin, Madison, WI

Applying guilds to any particular group of animals requires not only some idea of the concept, but a fair amount of information on the natural history of the organism(s) to which it is being applied. If one wants to define a functional unit that is useful for answering some questions, then one must know how to look at the groups and their natural history to be able to make these functional classifications. The natural history of birds is far better known than for many other groups. Generally mammals and vertebrates are still known better than many others, and the ability to make better assessments in advance of more detailed information would be nice to have.

There are some groups whose functional patterns and feeding patterns could be observed and some natural dichotomies noted, such as flycatchers and swallows. Flycatchers take items from the air by sitting in one spot and then sallying out, grabbing an item, and returning to the spot or watching space. Swallows fly around continuously, taking items while in flight. If the feeding patterns of groups of animals are followed, many species of both swallows and flycatchers will be observed, and it will be noted that flycatchers rarely fly around continuously like swallows, and do so only when there is an extremely high density of insects. Swallows rarely ever fly like flycatchers. There are very few birds around that perform both of these functions very often. If a large number of birds are using the air as a resource, one will find a natural dichotomy like the flycatcher and swallow strategies. If this dichotomy is extended into other groups, other types of breaks will be noted, although some are far less obvious. For instance, some foliage-gleaning birds which normally pick food items off branches will occasionally fly out to get something. The American redstart does some gleaning and a lot of flycatching. If one goes through a long line of birds, a continuum of a certain amount of flycatching and of gleaning will be noted; however, there are still a large number of birds that fit into one group or another, allowing a chance to make some natural, functional dichotomies.

Titmice, chickadees, nuthatches, and creepers all glean foods off surfaces of either small or large perches. These overlap quite a bit, so defining a guild is very difficult in a situation like this. It depends on the question. One could categorize all of these species as a type of surface bark and twig-gleaning guild. One could separate a group as being twig-gleaners, but in fact some of them like to spend time on twigs. Birds like the titmouse spend a fair amount of time on bark, and so does the chickadee at times. One could go finer than that and say that the nuthatches have a peculiar way of using bark; they could go both up and down the bark, but most things cannot go down the bark. Thus, they might find other resources on the bark, unlike species such as the creeper, which just goes up the bark, so some people would separate these two.

Whether or not these types of detailed separations are made depends on the question being asked, and how those guilds are used will then depend on these generalizations. But defining these things in the guild provides a chance to look at communities as they change. Just looking at changes in guild composition can provide an important clue about what changes are happening to communities. In moving from large to small patches of habitat, or from places that are relatively intact to those that have been altered by high-grading or other modifications, guilds will be found to change. Comparing these communities by looking at the changes from one to another or by looking at proportions of birds in a particular guild will provide important clues, such as the organizing principles of the communities, what is happening to the communities, or what might happen if similar changes follow in other areas. The bottom line in doing these kinds of assessments still rests on the natural history. The next three papers in this section were prepared by people who have a great deal of experience in the field of applying this concept to birds in the field.

TECHNIQUE FOR STRUCTURING WILDLIFE GUILDS TO EVALUATE
IMPACTS ON WILDLIFE COMMUNITIES

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The presentation of Henry L. Short and Kenneth P. Burnham has been
published as USDI, Fish and Wildlife Service, Special Scientific Report -
Wildlife No. 244 and is reprinted in Appendix A.

POTENTIAL APPLICATION OF THE GUILD THEORY CONCEPT
IN MANAGEMENT OF BIRDS OF THE WESTERN UNITED STATES

Jared Verner, U.S. Department of Agriculture, Forestry
Sciences Laboratory, Fresno, CA

THE USE OF GUILDS IN FOREST MANAGEMENT

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SESSION III. GUILD APPLICATIONS TO MODERN MANAGEMENT PROBLEMS

INTRODUCTION

Peter B. Landres, Department of Biology and Ecology Center,
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I would like to make a few brief comments about some potential benefits and problems that I see in the use of the guild concept. The benefits of a guild analysis are twofold. First, it reduces the number of community components, thereby decreasing the variability and facilitating analysis of the system that is under study. Second, an importnt aspect about the use of guild analysis for modern management is that it ties the organism to the resource. This coupling seems to be what managers need and are looking for, that is, something that ties together what effect a given change of a resource has on the organisms that use that resource.

So far, we have heard a lot about the positive uses of the guild concept. To balance this perspective, I would like to explore some of the problems. First, there has been some disagreement about the definition of a guild. I think that the heart of this problem revolves around what to me seems to be an inherent contradiction in the original definition of the term "guild" as coined by Richard Root. This contradiction stems from the use of the phrases "similar way" and "taxonomically different organisms" in the original definition. The constraint of "similar way" in assigning species to guilds generally restricts the organisms that are being considered to be those from a similar taxocene. For basic ecological research, this restriction does not pose a problem because the researcher can propose very specific questions; for example, "How are resources partitioned among foliage-gleaning birds?" For management purposes, however, the effects on all the organisms that use a particular resource are of interest. Therefore, the restriction to organisms that use the resources in a "similar way" prevents a full examination of the effects of altering a resource, and imposes a severe limitation on the utility of guild analysis for management. An appropriate definition of a guild for management purposes would be to simply say that a guild is a group of organisms that use a similar resource, and to exclude the "similar way" of the original definition.

The resource axes used to define guilds is also an area of concern. The use of different resource axes to assign species into guilds can result in entirely different guilds. Defining which resources to use is probably the single most important part of a guild analysis and depends on what questions the manager is asking, the purposes of the investigation, and the types of resources that are being considered.

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*See also the article "Use of the Guild Concept in Environmental Impact Assessment," by Peter Landres, which is in Vol 7, No. 5 of <u>Environmental Management</u>, pp 393-398.

Another problem that was briefly touched on by Tim Moermond was the classification of species into guilds. Hank Short used cluster analysis, a technique that has been used often; however, there are some (usually unstated) problems associated with this technique. It is not statistically rigorous, and therefore has an unknown level of precision. Also, the distinction of guilds on the cluster analysis dendrogram is usually done subjectively, and is therefore open to different interpretations by different people.

There is also the problem of circularity in assigning species to guilds. Researchers typically start with species lists and then develop some scheme based on the use of particular resources in which to peg these species. Conveniently, that scheme then classifies all the species. Although this is extremely circular reasoning, it does not invalidate use of the guild concept. People who use guilds, however, must be aware of this circularity, and not impart undue ecological significance to the guild analysis.

Richard Root mentioned the art of doing both ecology and guild analysis. Many investigators do not realize the extent of the subjectivity involved in a guild analysis. When Root coined the term "guild" he probably had no idea that it would be used for management purposes. Only later did the applicability of this concept to management become evident. Because the guild concept is relatively new, many aspects of the concept are still undergoing scrutiny and development. As have many ideas that are currently being used, I think that the guild concept must go through a maturation period before it will be an effective tool for management purposes.

In closing, there are two additional points that I want to briefly mention. One is the use of the term "guilding". The term "guild" is a noun, not an adverb, and therefore "guilding" is a misnomer. As an analogy, when you read a book you are not "booking". In the same way, in my mind, there is no such term as "guilding". The other point I want to make is that I would not refer to the guild concept as a theory. Theory implies a whole body of logical thoughts embodied in a particular term or phrase. In the case of guilds, we have one concept, that is, the use of similar resources, and not much else. To state "guild theory" is to elevate guild analysis beyond its means, possibly leading to unwarranted confidence and misuse.

The reason I am making such critical remarks is that when taking the guild concept from ecology into management, managers must be very careful about some of the concept's limitations. Misusing some of these terms may allow researchers to use this concept in ways that are not entirely appropriate. With careful use, guild analysis may provide a useful tool for management purposes; with uncritical or inappropriate use, it may confound or delay sound resource management.

BIOLOGICAL MONITORING AND ASSESSMENT IN THE SOLUTION
OF ENVIRONMENTAL PROBLEMS

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Environmental problems encountered by human society have origins in two
primary types of events: (1) natural events (droughts, earthquakes, etc.,)
and (2) events precipitated by human activities. Both threaten the health or
well-being of human society. We can prepare for the former by careful
planning but we can avoid the latter by implementing sound programs of
environmental management. But that requires understanding of pattern and
process in biological systems and development of assessment and evaluation
procedures that assure protection of biological resources. Ecological studies
of population dynamics, community structure, and ecosystem function provide
the biological foundations for development of such procedures. Regrettably,
most ecologists have been reluctant to use their basic knowledge to develop
appropriate procedures.

Since mankind's many activities now play the major role in shaping
biological communities throughout the world, I am interested in using
ecological theory in an attempt to minimize those impacts and thus preserving
earth's life support system. Monitoring of biological systems is a very
effective and direct way to assess the impact of human activities. That
mankind needs that assessment is clear from the declines, and even
disappearance, of major societies that resulted, for all practical purposes,
from environmental disturbance. Perhaps the best examples are from soil
degradation in societies all over the world (Troeh, et al., 1980). Other
historical examples include construction of wooden ships, which depleted the
timber supply several hundred years ago; the Western World sent explorers
throughout the world to find more timber, and the depletion became more
widespread. A more recent example of the preceptions of environmental
problems was the reaction of both hunters and non-hunters to the decline in
the variety of wildlife populations in North America, particularly
waterfowl. These and other examples clearly demonstrate the need to assess
environmental impacts of human society.

In my opinion, the solution and prevention of environmental problems must
be guided by three fundamental principles: (1) the need to preserve human
health; (2) the need to preserve aesthetic, recreational, and other uses of
biological systems for direct human benefits; and (3) probably most important,
the need to preserve life support systems that provide both goods and services
to human societies through the maintenance of healthy ecosystems. We
obviously are very dependent on those systems.

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The Guild Concept

The origin of the guild concept in ecology is rooted in population biology and the niche concept (Root, 1967). Careful application of this concept offers an opportunity to reverse the trend toward environmental decline (Landres, 1984; Severinghaus, 1981; Verner, 1984). Yet, like any tool of technological society, use of the guild concept has both strengths and weaknesses. The greatest weakness could develop if we turned exclusively or even dominantly to the use of guilds as our way of making decisions about management of environmental problems. If that happens, we would repeat the mistake of 15 to 20 years ago when there was excessive dependence on a number of indexes of diversity (e.g., Shannon-Weiner function). If we adopt guilds as a simplistic surrogate of environmental quality, we could lead ourselves into similar problems.

A more rigorous and ecologically sound approach is clearly needed. Here, I would like to cite several examples from my own experience to show that the concept of guild, or ecological classification in a broader sense, should be a strong component of biological monitoring and assessment.

Water Resources, Guilds, and Fish Communities

My first examples come from the field of water resource management. Since the time before European man came to the New World, the surface waters of the United States absorbed the effluents and other impacts of a developing society. More recently, a "dilution is the solution to pollution" approach to waste disposal prevailed and typically resulted in grossly polluted water and associated losses of a variety of aquatic resources, particularly fish. By the mid-twentieth century, legislative efforts were initiated to reverse this ominous trend. Those efforts produced programs to improve water quality. Most of the decisions about how those programs were to be developed focused on physical/chemical parameters of water resource systems (e.g., dissolved oxygen, nitrogen, phosphorus, and heavy metal content). Physical/chemical parameters were used as surrogates of biological integrity, with the assumption that if we could correct physical/chemical problems, we would ensure biological integrity. But chemical monitoring misses many of the human-induced perturbations that impair uses of water (Thurston, et al. 1979; Karr and Dudley, 1981). Since biological problems are at the center of most environmental problems, we should focus more directly on biological monitoring.

Recent work with fish communities demonstrates the value of including selected ecological classifications (guilds) to analyze degradation in water resource systems. The first study I will mention is analysis of the Maumee and Illinois Rivers (Karr, et al., 1985) where we examined changes in the fish faunas since 1850. We evaluated how the populations of various fish within those two river systems have changed since 1850. Because the Illinois River watershed was the largest (Table 1), it supported more species (141 vs. 96). Further, with proportionately more "large river" miles, the "large river" areas of the Illinois supported more fish species than did the Maumee.

Our more detailed analysis assessed population trends over the last century in five classes: extirpated from the watershed, declining, stable, increasing, and introduced. For simplicity, I combine these into three

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classes here: increasing, stable, and declining (Table 1). A majority (67 percent) of fish species in the Illinois watershed have declined, with fewer but still a substantial number (44 percent) having declined in the Maumee River.

When the fish are classified according to the size of the river that they frequent (headwater, mid-river, large river), many species declined in all size classes (Table 1). However, in the Maumee, headwater regions were most impacted. As one moves downstream, extirpations and declining species decrease in proportion. In contrast, the Illinois River exhibits very high levels of species with reduced populations throughout the three size classes of rivers!

Additional analysis using a guild-based approach yielded insights about both patterns in fish communities of disturbed areas and the processes that produce them. We looked at the guild structure of species that were declining or extirpated from each of these river systems. For headwater, 11 species declined in the Maumee River system, most of which depended on invertebrates for food. No omnivores or planktivores declined, and only one herbivore declined. The Illinois River again had the highest number of declining

Table 1. Characteristics of the watersheds and fish faunas of the Maumee and Illinois rivers. (Modified from Karr, et al., 1985)

	Maumee	Illinois
BASIN AREA (km^2)	17,100	72,300
DISCHARGE (m^3/s)	134	633
NUMBER OF SPECIES		
Large river	16	40
Mid-river	54	56
Headwater	28	39
Total	98	135
PERCENT OF SPECIES		
Declining	44	67
Stable	35	23
Increasing	21	10
PERCENT OF SPECIES DECLINING OR EXTIRPATED		
Large river	31	60
Mid-river	44	73
Headwater	50	64
TOTAL	44	67

species, especially species feeding on invertebrates. Species from all guilds exhibited significant declines in the Illinois River (Karr, et al., 1985).

We then analyzed human impacts that might be responsible for these alterations in guild patterns. Research in recent years has shown that a complex of ecological interactions are altered by human activities and many of these affect the guild structure of aquatic communities. For example, in natural headwater streams in forested regions, most of the energy that feeds the stream community derives from leaves that fall into the stream. These are broken down by fungi and bacteria which, in turn, support healthy populations of invertebrates that are consumed by many fish. As a result, the dominant fish are invertivores and then invertivore-piscivores. Relatively few omnivores and herbivore-detritivores are present.

Alteration of a headwater stream by channelization or clearing of near-stream (riparian) vegetation alters the system's food base and the guild structure of the fish community. The community is changed to one dominated by omnivores and herbivore-detritivores, with a sharp decline in the invertivores and invertivore-piscivores.

Other effects of channel and riparian alterations include increased sunlight and increased availability of nutrients, especially in agricultural areas, that produce late summer algal blooms that choke the waterway and stress fish populations. This may also be accompanied by very high water temperatures. Finally, channel activities in headwater streams in combination with changes in land use produce more extreme drought and flood conditions.

Human impacts in the larger river system also produce changes in the guild structure of the community. A primary reason for the Illinois River pattern differing markedly from the pattern in the Maumee River is that early in this century, Chicago diverted its disposal of sewage from Lake Michigan (its water source) into the Illinois River. Subsequent increases in toxic effluents and the maintenance of the Illinois as a navigable river have also reduced fish populations. The resuspension of a variety of fine particulates destroys invertebrate communities and thus removes the food base of many fish species. Through an examination of the guild structure of these communities we can detect changes and interpret their causes.

Introduction of exotics also produced major changes in the fish fauna of the Illinois River, first as a decline in native fishes followed by major increases in the carp population. A major commercial fishery developed to harvest carp early in this century, but even this species has declined significantly due to toxics and habitat alteration. Historically, the Illinois River was the second largest commercial fishery in North America. The impacts discussed briefly above have decimated that commercial fishery (Karr, et al., 1985).

Analysis of these patterns in the Illinois and Maumee Rivers and other studies led me to seek an integrative index that would express the extent of degradation in an aquatic community. Historically, efforts to develop indexes for biological monitoring of water resources used benthic organisms, especially invertebrates and diatoms.

However, fishes seemed ideal for monitoring for a variety of reasons. Biological communities reflect watershed condition since they are sensitive to changes in a wide array of environmental factors. Fish involve species consuming at all trophic levels, and are relatively long-lived. For numerous other reasons, fishes are ideal as biomonitoring tools (Table 2). Thus, I sought a methodology to assess biotic integrity using fish communities. Such a methodology should integrate responses of biotic communities through an examination of patterns and processes from population, community, and ecosystem levels--an array of metrics for biology like the leading economic indicators so common in econometric analyses.

Using that approach, I developed an Index of Biotic Integrity (Karr, 1981; Fausch, et al., 1984) using data from collections of entire fish communities. Results are summarized as 12 ecological characteristics, or metrics, which can be classified into three major groups: species richness, trophic composition, and fish abundance and condition. In the aggregate, these 12 metrics include, but are not limited to, use of guild concept in assessing environmental degradation. The metrics chosen for this analysis are measurable attributes of the community that are correlated with biotic integrity, which is not directly measurable.

With this index, we were able to show that a small stream channel reconstruction project seriously reduced biological integrity in an Indiana stream (Figure 1) and that chlorination in secondary treatment has major negative effects on biotic integrity (Table 3) while addition of tertiary treatment to remove ammonia does not increase biotic integrity (Table 3) above that derived from unchlorinated secondary effluent.

This index is now being used by a number of state and Federal agencies in water resource assessment and planning. Its strengths, like the strength of econometric models with several major metrics being included (GNP, industrial production, wages, etc.), include its broad ecological foundations. Ecologists must develop assessment tools that depend on direct biological monitoring of several metrics, rather than rely on one metric, such as a diversity index or guild structure of the community. After all, ecological systems are every bit as complicated as economic systems.

Guilds and Bird Communities

Use of the guild concept in ecological studies originated in studies of niche structure of avian communites (Root, 1967). Since that seminal paper, numerous theoretical papers using the guild concept have appeared. Most early papers using the guild concept in studies of bird communities were oriented toward the analysis of food and other resources partitioning. Recently, several workers have used guild structure as a way of evaluating human influences. The most common examples come from the analysis of impacts of forestry practices (Verner, 1984).

Table 2. Advantages of using fish as indicator organisms for assessment of
          biotic integrity.

1. Life-history information is extensive for many fish species, especially
    commercial and sport fishes and at least some information is available on
    virtually all North American species.
2. Fish communities generally include a range of species that represent a
    variety of trophic levels (omnivores, herbivores, insectivores,
    planktivores, piscivores). Their occupation of positions throughout the
    aquatic food web provides an integrative view of the watershed.
3. Relative to diatoms and invertebrates, fish are relatively easy to
    identify and technicians require relatively little training. Indeed,
    most samples can be sorted and identified at the field site with release
    of study organisms after processing.
4. Evaluation of biotic integrity can be made very rapidly in most cases.
    No long-term laboratory work is required that is often delayed due to
    other demands. (How many unprocessed invertebrate samples sit on
    laboratory shelves?)
5. The general public can relate to statements about conditions of the fish
    community. The results of studies using fish can be directly related to
    the aquatic protection mandate of Congress. Monitoring of fish allows
    direct assessment of resource potentials that cannot be tested when other
    taxa are utilized in a monitoring program.
6. Both acute toxicity (missing taxa) and stress effects (depressed growth
    and reproductive success) can be evaluated. Careful examination of
    recruitment and growth dynamics among years can help to pinpoint periods
    of unusual stress.
7. Fish are typically present, even in the smallest streams and in all but
    the most polluted waters.
8. Fish population and/or community data are already widely collected each
    year by fish and game departments, university ichthyologists, and others
    interested in stream biology. Unfortunately, these data bases are often
    poorly used in the process of environmental quality evaluation. The
    question then becomes not, "Should we collect data on fish?", but rather,
    "How can we improve the quality of fish data we collect and best use
    those data that are already being collected?"
9. Most fish reproduce one time per year at a set spawning season and are
    relatively stable during the summer when most sampling activities occur.
10. Fish species respond to relatively macroenvironmental influences rather
    than to micro-environments typical of algae and invertebrates.
11. Fish are relatively long-lived and thereby provide temporal integration
   of stream environments.
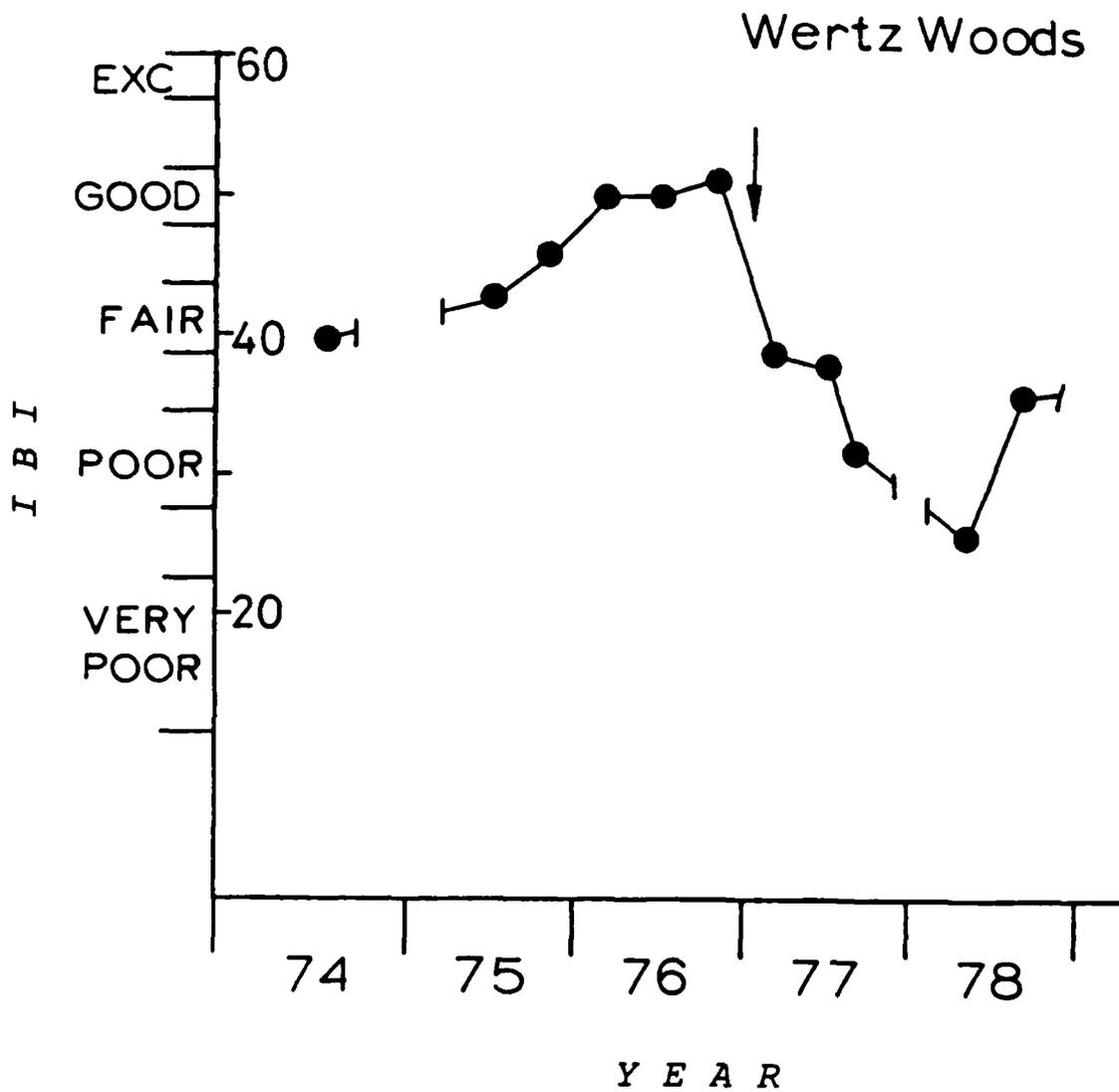
Figure 1. Changes in index of biotic integrity (IBI) over time in Wertz
Woods, Back Creek, Allen County, Indiana. Note sharp decline in
IBI from Good to below Poor following Wertz Branch channel work
(indicated by arrow) late in 1976.

Table 3. Index of Biotic Integrity ($\bar{x} \pm$ sd) downstream of wastewater treatment plant during three types of wastewater treatment. Release of chlorinated secondary effluent (Phase I), unchlorinated secondary effluent (Phase II), and unchlorinated secondary and tertiary nitrification effluent. (Modified from Karr, et al., ms.)

Stream	IBI Values		
	Phase I	Phase II	Phase II
Copper Slough	28.6 ± 8.3	41.6 ± 3.2	40.1 ± 4.0
Saline Branch	29.2 ± 3.2	31.7 ± 4.0	32.7 ± 2.4
Kaskaskia Ditch	33.1 ± 7.7	37.9 ± 3.9	39.3 ± 3.5

Here I illustrate use of the guild concept in developing environmental insight from my own experience with studies of bird communities. When one uses mist nets to sample birds in the undergrowth of forest, a community of sorts is defined by the captured avifauna. For statistical purposes, I operate nets for 3 to 5 days until I have recorded 100 captures. Each species is classified according to its food habitats and foraging location. The configuration of the resultant bar graph (Figure 1) is referred to as a "guild signature" (Karr, 1980).

In the lowland forest of central Panama, the sampled avifauna shows strikingly similar guild signatures over three dry seasons (Figure 2). Samples from other regions (Africa, Southeast Asia, North America) illustrate other patterns and establish standards that vary among region and habitat types (Karr, 1980). If a sampled community diverges significantly from the standard, one might then ask: "Why is that case? Does it result from a human impact, a peculiarity of that environment, or something else?"

If we hope to use guilds as a way of evaluating expectations in certain kinds of communities, we must look more carefully at this kind of analysis. How would deciduous forests around North America look? How different would coniferous forests and deciduous forest systems be? Can we identify particular characteristics of those different kinds of forest (or other non-forest) ecosystems? Then the next step (and this is the important step from

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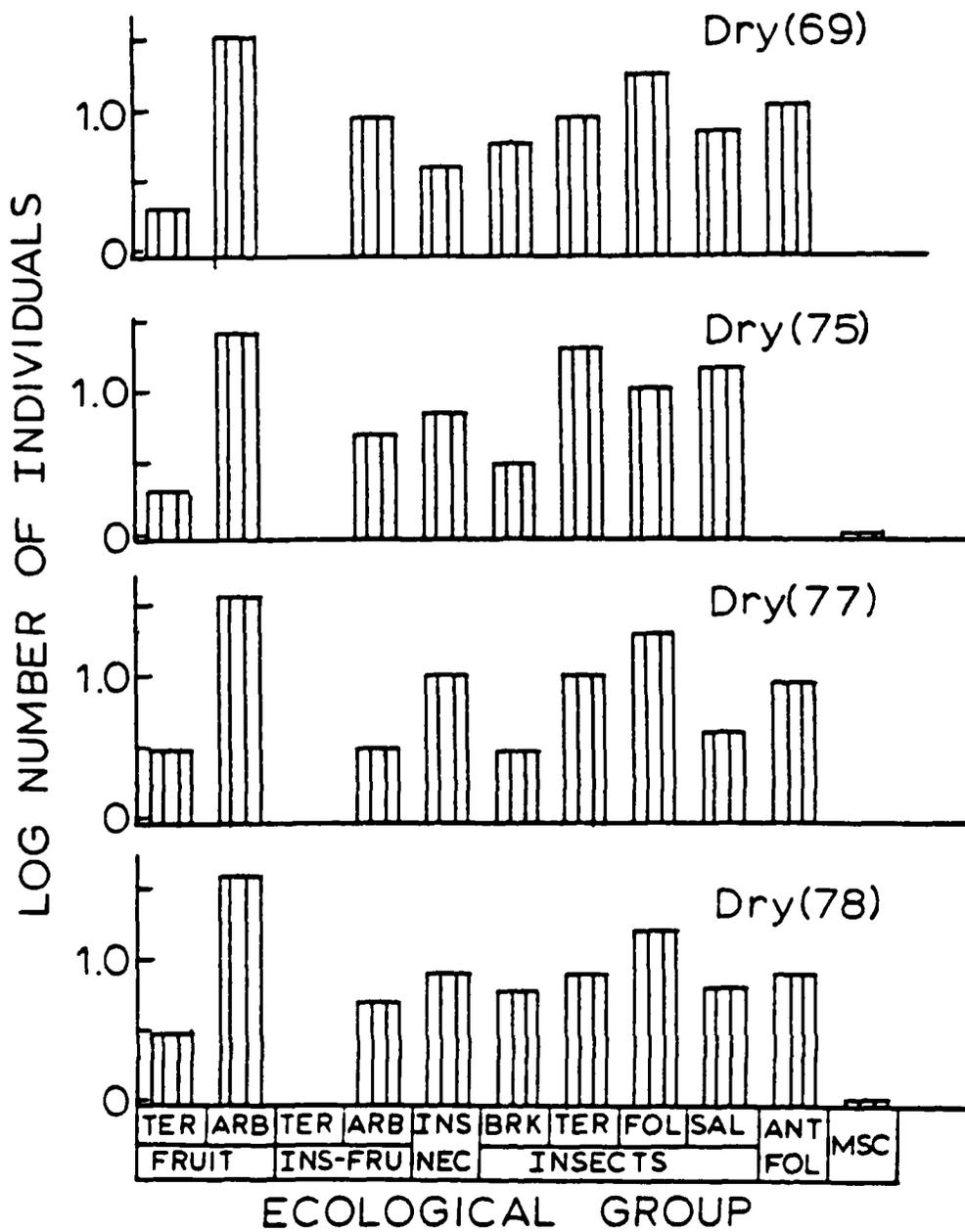
Figure 2. Guild signatures for tropic groups in undergrowth mist-net samples of birds from tropic forest in central Panama.

the standpoint of biological monitoring, assessment, and management) is how do
these things get perturbed as a result of various activities of man? We can
use this information to identify systems that have some stress which is
reflected in a guild signature, and/or we can predict the specific outcome (in
terms of the guild structure of the modified community) of certain management
regimes.

During the course of studies of tropical forest birds in several
geographic areas, I had an opportunity to sample in two Malaysian forests.
The Bukit Lanjan Forest was the site of intensive studies by a variety of
biologists, notably mammal specialists, but also plant and bird specialists.
In contrast, the Pasoh Forest was relatively undistrubed. I sampled with mist
nets in both of those forests and found a striking peculiarity in the guild
structure of the community at Bukit Lanjan.

The sample size in these two sites, although small, was similar with 40
and 36 captures (Table 4). The species richness was 35 percent higher, and
capture rates were much lower at the less disturbed Pasoh Forest. However,
when one looks more carefully at the guild structure of the two communities, a
clearer view of the differences emerges. The areas are strikingly similar in
number of species of foliage insectivores and insectivore-nectarivores.
However, the number of captures of insectivore-nectarivores is very different,
with seven times as many caught at the disturbed Bukit Lanjan site. Thus, the
Bukit Lanjan site had reduced species richness, low capture rates, and an
unusual abundance of insectivore-nectarivore--a spider hunter. Apparently,
the continuous and regular activity of many research biologists created a
variety of openings in the forest undergrowth, which resulted in the
colonization of plants that were particularly well adapted to that kind of
habitat. Those were the flowering plants that depend greatly on that

Table 4.   Comparison of undergrowth avifaunas of two Malaysian forests.
            Data are based on mist-net samples of birds.

Metric	Bukit Lanjan	Pasoh
Number of:		
Captures	40	36
Species Represented	11	15
Capture Rate		
(Captures per 100 net hours)	25	12
Guild Structure		
Number of Species		
Insectivore-Nectarivore	1	1
Foliage Insectivore	9	10
Sallying Insectivore	1	4
Number of Individuals		
Insectivore-Nectarivore	22	3
Foliage Insectivore	17	23
Sallying Insectivore	1	4

particular species of bird. Thus, we have a research project designed to understand something about the structure of biological systems, but which was so intense that it perturbed the trophic structure of the communituy.

The message for me was to find another site for my field studies. The coordinators of the long-term research in that area might use these results to reassess their project activities and goals. Their activities were very likely changing the nature--the structural characteristics--of their study communities.

In another area--central Panama--I have been particularly interested in the avifauna of a man-made island in Gatun Lake, a lake created by the damming of the Chagres River to produce the Panama Canal. Although this island is isolated from the nearby mainland by only a few hundred meters, 50 to 60 species of forest birds are missing from this island because of its isolation, small geographic extent, and limited availability of sheltered areas along stream channels (Karr, 1982a, 1982b). I compared the birds on this island to birds of the nearby mainland forest adjacent to the island, which, in fact, was certainly connected to the island before the Canal was created.

Which species are missing from the island and are they a random selection of species found on the adjacent mainland? With respect to food type, I was unable to reject that random subset hypothesis, that is, the percentages of species in each guild are indistinguishable.

However, when one uses guilds based on where the birds feed in the vegetation column (bark, terrestrial, undergrowth, canopy, etc.), island and mainland distributions of species are significantly different (Table 5). Species on Barro Colorado that are missing tend not to be canopy species. Rather, they tend to be undergrowth species and terrestrial species, while species that glean arthropods from the bark are missing in a proportion which is just about what would be expected at random. Thus, there are several ways we can look at guilds, whether we call them guilds or groups. Some may and some may not provide us with insight about why, how, and what kinds of species are missing; looking at only one or the other might prevent us from finding solutions to problems or to understanding why particular patterns exist.

When I realized that primarily undergrowth and ground species were missing, I monitored the populations of those species. Using eight dry seasons of data, species that are missing from Barro Colorado Island tend to have significantly more variable populations on the mainland than the species still present on the island (Table 6). Therefore, a good predictor of extinction first defines a species as one living in the undergrowth and second as one that tends to have a variable population level. In addition, the population variability is not strongly correlated with abundance, so what we have here is a real change in populations on a year-to-year basis in tropical forest, and that tells us something about why particular species are missing.

As a final example of use of guilds in the study of human impact on bird communities, I draw on work in forest patches isolated in a sea of agricultural land (primarily corn and soybeans) in Illinois. Smaller forest areas support many fewer species than larger areas, much as Barro Colorado Island supported a depauperate avifauna. Forest interior species tend to

increase in species richness as one goes across the size gradient (forest patches of 1 to > 600 ha), and forest edge species tend to decrease (Blake and Karr, 1984). In addition, the guild structure varies with island size, the most notable shift being a decrease in the more opportunistic omnivores as island size increases (Figure 3). Disturbance that creates habitat islands alters the food base in smaller patches, much as channelization of streams increased the species richness and abundance of omnivores in headwater streams.

Table 5. Primary stratal association for resident land birds in mainland forest near Barro Colorado Island (BCI) and for species on mainland not present (extirpated) from BCI.

	Stratum				
Status	Canopy	Undergrowth	Ground	Bark	Total
All mainland residents	121	76	26	14	237
Extirpated from BCI	11	23	13	3	50
% extirpated	9.1	30.3	50.0	21.4	21.1
% relative to expectation from total	Low	High	High	Equal	—

Table 6. Variability in populations of birds in forest at Limbo Camp, Parque Nacional Soberania, Panama over eight dry seasons. Two groups of species are identified: those still present on Barro Colorado Island (BCI) in Gatun Lake and those no longer present on BCI. (Modified from Karr, 1982b).

		Coefficient of Variation--Number of Captures	
Status on BCI	Number of Species*	All Species	Insectivore Species
Present	21 (12)	86.3	93.4
Not Present	17 (15)	123.7	127.8
		$p < .005$	$p < .005$

* All Species (Insectivorous Species).
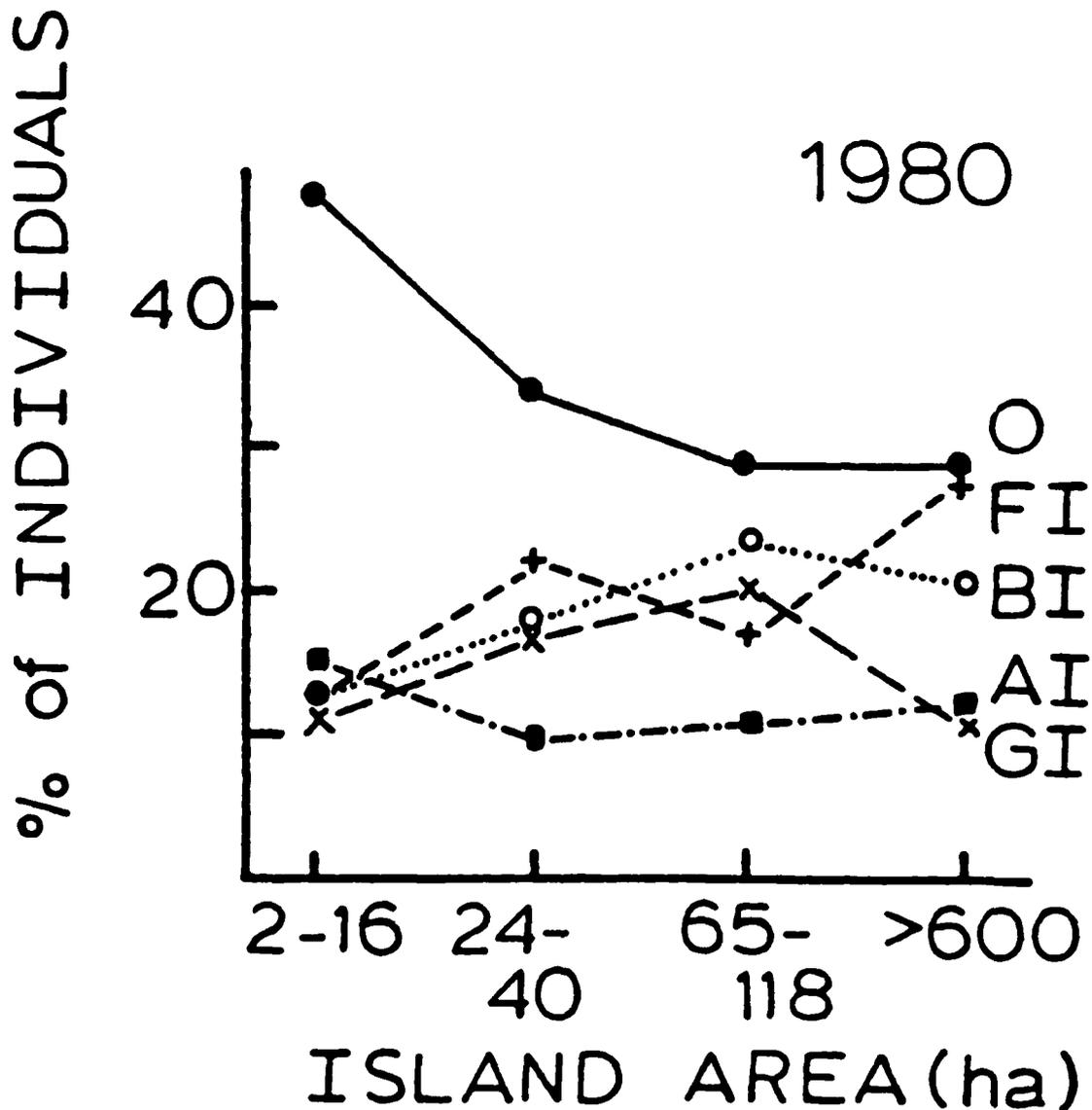
Figure 3. Percent of individuals in several trophic groups for birds of
forest islands of various sizes in east-central Illinois.
O=Omnivores; FI=Foilage Insectivores; BI=Bark Insectivores;
AI=Aerial Insectivores; and GI=Ground Insectivores. (Modified from
Blake, 1983.)

Summary

With these selected examples I have tried to demonstrate: (1) the value of examining biological communities from the perspective of their ecological organization (guild structure) and, of equal importance (2) the need for biological assessment to use a broader set of metrics than ecological guilds. Insights about environmental problems can best derive from consideration of guilds as well as other population, community, and ecosystem perspectives. Guilds provide an important tool for monitoring, assessing, and evaluating biological systems. However, use of guilds should be coupled with a variety of other ecological insights, or we will have the same problem we had with diversity indexes. In all cases, these biological insights are extremely important for making these decisions, rather than use of only some arbitrary number or value.

With insightful use of our biological knowledge, we should ultimately be able to make reliable predictions rather than only after-the-fact judgments. I think some prediction is possible even now; biologists seem hesitant to make predictions, although other disciplines, like economics, regularly produce predictions. I think our track record would be at least as good as those of the economists. In one study, it was shown that the National Bureau of Economics, using the most powerful econometric models and with a massive data base, has failed in 80 percent of its latest predictions of even the sign of change of the gross national product (Business Week 2698: 11; 27 July 1982). Surely, we can do that well in ecology and we should not apologize if we are not absolutely correct in each prediction. Our reluctance to make predictions in the absence of absolute accuracy contrasts strikingly with the willingness to make predictions within other disciplines.

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POTENTIAL APPLICATIONS OF GUILD CONCEPTS IN NATURE PRESERVE
MANAGEMENT AND MINED-LAND RECLAMATION:
THE FUNCTIONAL GUILD CONCEPT

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The guild concept is used to summarize ecological relationships among organisms. The concept has been applied to many organisms based on similarity in trophic apparatus, feeding behavior, habitat utilization, prey selection, and other criteria. Such guilds as the ground-brush-foraging birds, sap-feeding insects, and insectivorous mammals are easily recognized as potential guilds. However, plant guilds are less obvious and more difficult to define in an accurate and meaningful way.

Plant groups such as trees, shrubs, herbs, and grasses are familiar. Plant growth forms may not be related to use of environmental resources or accurately characterize ecological differences among plants, and therefore should probably not be used for guilding criteria. Plants respond to their environment by changes in metabolism, resource utilization, or morphology, but guild designations usually suggest unchanging relationships. Once species are placed in guilds, loss of information can occur if guild responses rather than species responses are studied. Guilds can be misleading if a species is assumed to conform to all guild criteria because guild criteria do not account for species-specific attributes. These problems are more likely to surface with plants than animals due to our greater ignorance of plant environmental requirements, physiology, and ecology.

One major system for designating plant guild categories has been developed (Grime, 1979). Plant groups representing the extremes in ecological and reproductive strategies were defined. The system is theoretically based on plant responses to stress and disturbance. Stress was defined as "a phenomenon restricting photosynthetic production" and disturbance as "a factor responsible for the partial or total destruction of plant biomass." On the basis of these two variables, Grime defined four basic environments and plant responses, each potentially equivalent to an ecological guild. These include:

1. Environments with high disturbance and high stress where conditions are inhospitable for plant growth.

2. Environments with high stress and low disturbance, such as deserts or arctic tundra, or areas where plants would be subjected to extremes in nutrient stress, where the successful strategist is the stress-tolerant plant, able to survive with minimum resources.

3. Environments with low stress and high disturbance, like productive agricultural soils, where the successful plant guild would consist of opportunist weedy plant species.

4. Environments with low stress and low disturbance where plants capable of growing in high-density and competing for abundant resources would be favored. In such areas, quick regeneration, establishment, or invasiveness by a complex of growth and reproductive mechanisms are characteristic of successful plants. A number of intermediate strategies, such as the stress-tolerant opportunist species, were conceptually defined by Grime.

Grime's system, like other attempts at plant guilding, has several problems. The categories are confusing, because plant responses overlap greatly. Guild categories are general, and there are no obvious cutoff points to determine when one strategy becomes another. In addition, this system suffers from the assumption that stress and disturbance are independent variables and that they can be measured in accurate and meaningful ways. Measurements of stress and disturbance are difficult, and their meaning is questionable. A stress to one plant may be a disturbance to another plant, or to the same species in a different phenological condition or ecological setting. Plant responses are difficult to evaluate, which is a serious limitation toward successful guilding of plants. Greenhouse experiments may not represent field situations and should not be the primary basis for placing plants into guilds. Before a guild system becomes useful for management, volumes of data on plant species responses to controlled field and laboratory studies must be reviewed.

Simplistic classification approaches for plants such as into perennial, biennial, or annual categories can be confusing and may not apply in different areas, even for the same plant species. This is especially true for species that exploit ephemeral habitats. Such species change very quickly to take advantage of short-term environmental changes. A guilding protocol would have to account for this variability.

Plant biologists work with many plants and are forced to simplify, condense, and integrate data. We have adopted a simple use of the guild concept for plants by assigning categories based on response to our objectives and land management goals. We have coined the term "functional guild," since the categories we assign reflect how plants function from an ecosystem management perspective. We create artificial guilds of plants based on similar **ecological** responses to habitat disturbance, land management strategies, or the benefits plant species offer in ecosystem rehabilitation.

This guilding approach is illustrated with two case studies. The first involves management of the 2.1-ha James Woodworth Prairie Preserve, Niles, Illinois—a tract of tall-grass prairie refuge. The guild concept was used to define a system of plant classification based on the ways the plants respond to anthropogenic and natural disturbances, and on the desirability of plants from a prairie preserve manager's perspective. As managers, we attempt to preserve and enhance natural patterns of vegetation and native plant species diversity. We have classified and mapped the 207 plant species present into three general guilds: the native or desirable prairie plants (Figure 1); native weeds which are native North American plants, possibly from the prairie biome, that can present problems and require management attention (Figure 2); and the naturalized plants or exotic plants (Figure 3), imported from outside the area, which management strives to selectively eliminate (Apfelbaum and Rouffa, 1982). From historic aerial photographs, and five years of field studies, the recent disturbance history of the preserve is known.

Disturbances include the installation of clay draintiles in the 1930s, which significantly altered soil profiles and vegetation; installation of a sewer line in 1971, which has had a similar effect; vehicle traffic, which caused local soil compaction and ponding problems; and several other disturbances, including administered fire. Some plants have benefited from disturbances (Figures 4 and 5).

With information on plant responses to these disturbances, and on plant desirability, guilds have been designed to aid management of the preserve. Various methods are used to manage the preserve and to monitor management effects (Apfelbaum and Rouffa, Ibid). Isopleth maps from 230 1-meter-square permanent sample quadrats located on a regular 10- x 10-meter grid are generated and show where different management strategies may be required, based on locations of undesirable species or groups of plants. Data on plant cover, frequency, and importance value are used in conjunction with these maps to further focus management. Use of clearly defined functional guilds and graphics support the use of specific management strategies in localized areas, and consequently, much more precise and effective management.

We have also used a guild concept in reclamation of mined-lands in Wisconsin and Michigan. Mine reclamation often establishes vegetation on rock substrates without organic materials, poor nutrient supply, and no seed bank.

Unlike nature preserve management, mine reclamation strategies must be responsive to various legal mandates. Some laws require establishment of a vegetation of native plant species that will become similarly productive to pre-mine conditions. In Wisconsin, the administrative code for metallic mining reads as follows: "All disturbed surface areas shall be revegetated as soon as practicable after disturbance to stabilize slopes and prevent air and water pollution, with the objective of reestablishing a variety of plants and animals indigenous to the area immediately prior to mining, unless such reestablishment is inconsistent with the provisions of State Code 144.81 (15). Plant species not indigenous to the area may be used if necessary to provide rapid stabilization of slopes and prevention of erosion, if such species are acceptable to the Department, but the ultimate goal of reestablishment of indigenous plants shall be maintained" (NR 132.09).

For reclamation we chose groups of plants and a reclamation program design that responds to the realities of mine reclamation, biology, and applicable laws (Ludwig and Apfelbaum, 1981). We have found mandates are often directly in conflict with the biological realities, since the legal requirements may be impossible to achieve in the short term. For example, providing maximum erosion control and establishing populations of indigenous plants at reasonable costs from our experience are mutually exclusive due to the time required by the desirable native plants to establish and grow an erosion controlling cover. The guild concept has helped us to respond to legal issues and design reclamation programs that work mostly by enabling clearer communication with regulatory agencies on our reclamation strategies. This includes addressing a complex and often mutually exclusive mix of goals in the short and long term.

We have conducted reclamation research using native plants, mixes of native and agricultural plants, and only agricultural plants in various combinations on ferrous waste rock material slopes. We have found that the

species that are planted determine the rate and direction of plant succession (Figure 6) and the ultimate responsiveness of a planting to the law. Previous plantings at the mine showed erosion control was most rapid and effective in the short term with initial plantings of crown vetch (Coronilla varia), alfalfa (Medicago sativa) or bird's foot trefoil (Lotus corniculatus). These Eurasian legumes all formed a dense productive cover within two growing seasons. However, vetch and alfalfa strongly inhibited invasion by native plants and conflicted with mandated requirements for indigenous vegetation. We found agronomic plants to often not offer the best erosion control in the long-term, especially during drought periods when native plants were favored. Plantings of only native species resulted in the least effective short-term erosion control, highest costs, and lowest invasion rates.

Our studies have led us to choose short-lived agronomic plants that function to control erosion quickly and later promote plant succession. The plant species chosen for revegetation depends on microsite parameters, including substrate surface temperatures, moisture availability, evaporative water loss rates, slope aspect, growing season length, substrate chemistry, and other variables. It is essential to evaluate a plant species' capability and ecological response in test situations before choosing species that will satisfy mine reclamation requirements. Characteristics such as plant dormancy or germination requirements, reproductive strategies, nutrient requirements, and compatibility with other plants in the short and long term (aggressiveness and persistence) must be considered in the design of realistic functional guilds for plants in mined-land reclamation.

In conclusion, functional guilds, perhaps more than other uses of ecological guild concept, must be designed on a case-by-case, site-specific basis. Nature preserves and mines require customized management. Because different assemblages of plants have variable relationships with other organisms and the abiotic environments, simple transfer of findings and technology from one location to another is usually not entirely possible or desirable. Lastly, due to the site-specific nature of functional guilds, experimentation and baseline research is critical for success in each area.

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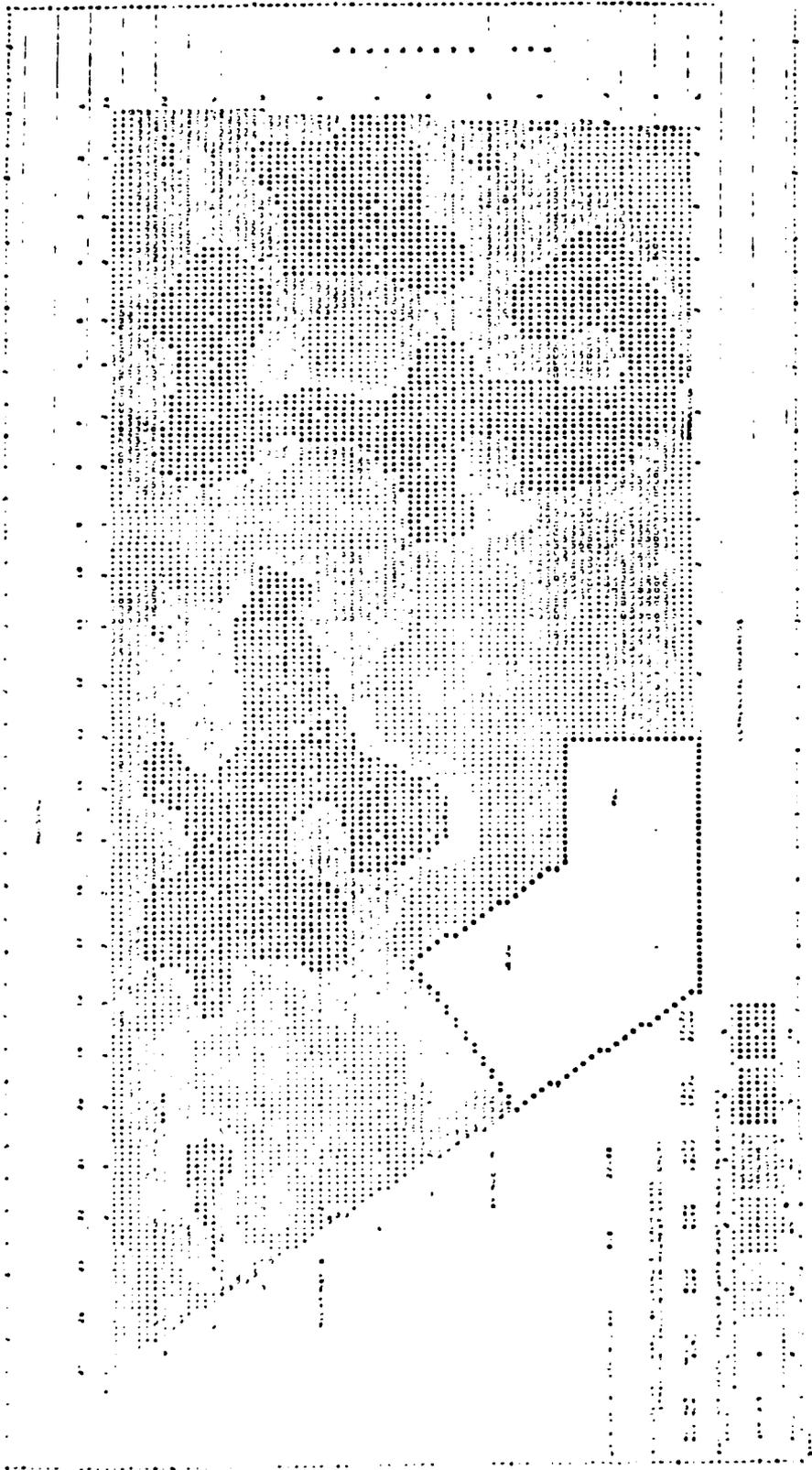
Figure 1. Isopleth map depicting native plant species diversity (richness) in the James Woodworth Prairie Preserve, Niles, Illinois, in 1979. Species richness over 230 m^2 quadrats was punched and run through Harvard's Symap software to generate this map. Least diverse areas are wetlands dominated by blue-joint grass (Calamagrostic canadensis [Michx.] Beauv.), while the more diverse areas often had more than 20 species per square meter. An interpretive building (BLDG) and parking lot (PKG) are in the fenced prairie. This is a five-level symap.
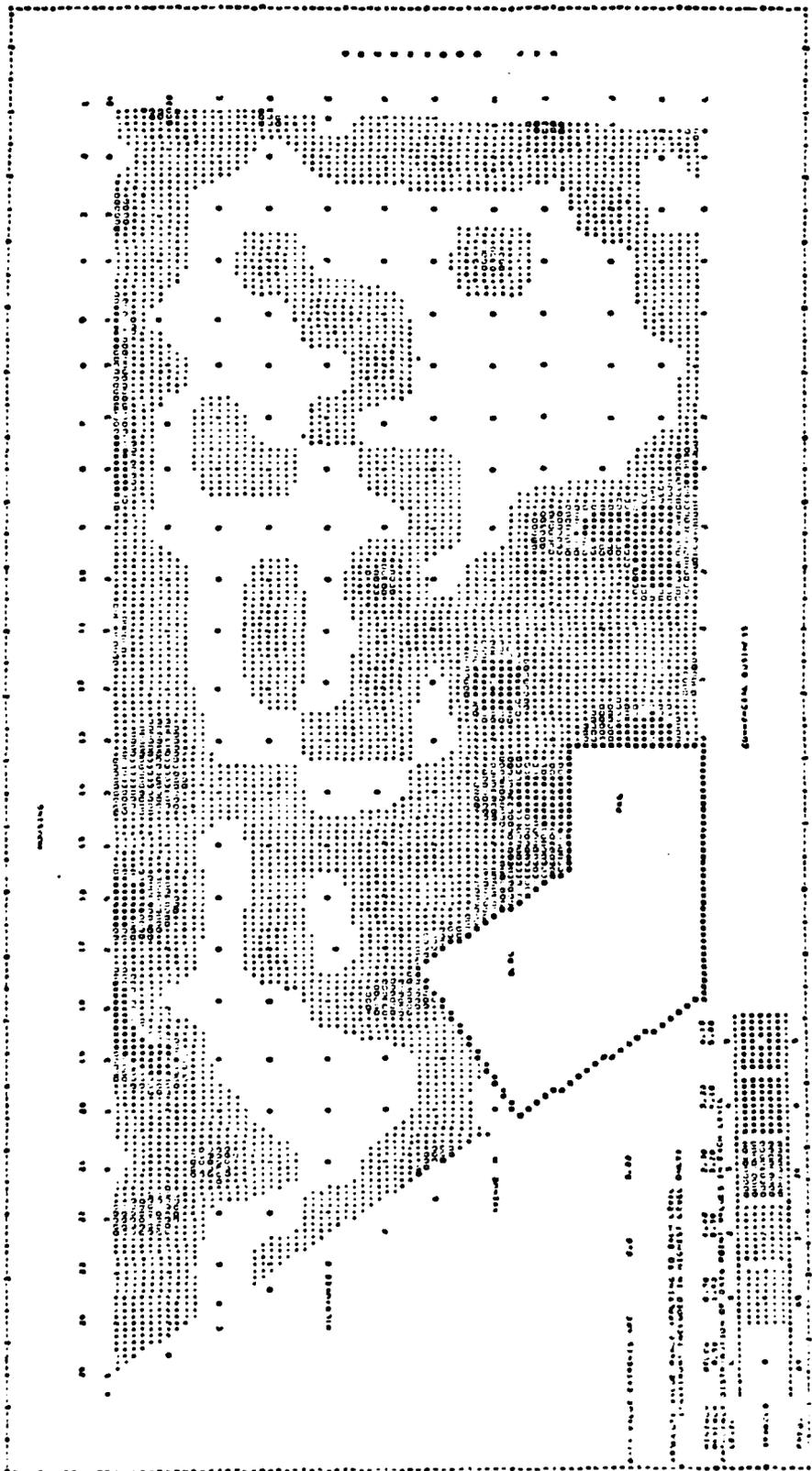
Figure 2. Patterns of native-weed species richness in the Woodworth Prairie, July 1979. In comparison to the isopleth map of non-native weeds, this map shows that native weeds behave differently in the preserve. However, richest areas are also located in areas subjected to disturbances. Segments of an abandoned figure eight go-cart track are especially conspicuous just east of the parking lot.

Figure 3. Patterns of non-native plant diversity in the James Woodworth Prairie Preserve, Niles, Illinois, in July 1979. Richest areas are associated with disturbances along fence lines, the interpretive building, parking lot, and along historic vehicular intrusions, a sewer line, an abandoned go-cart track, and other disturbances.
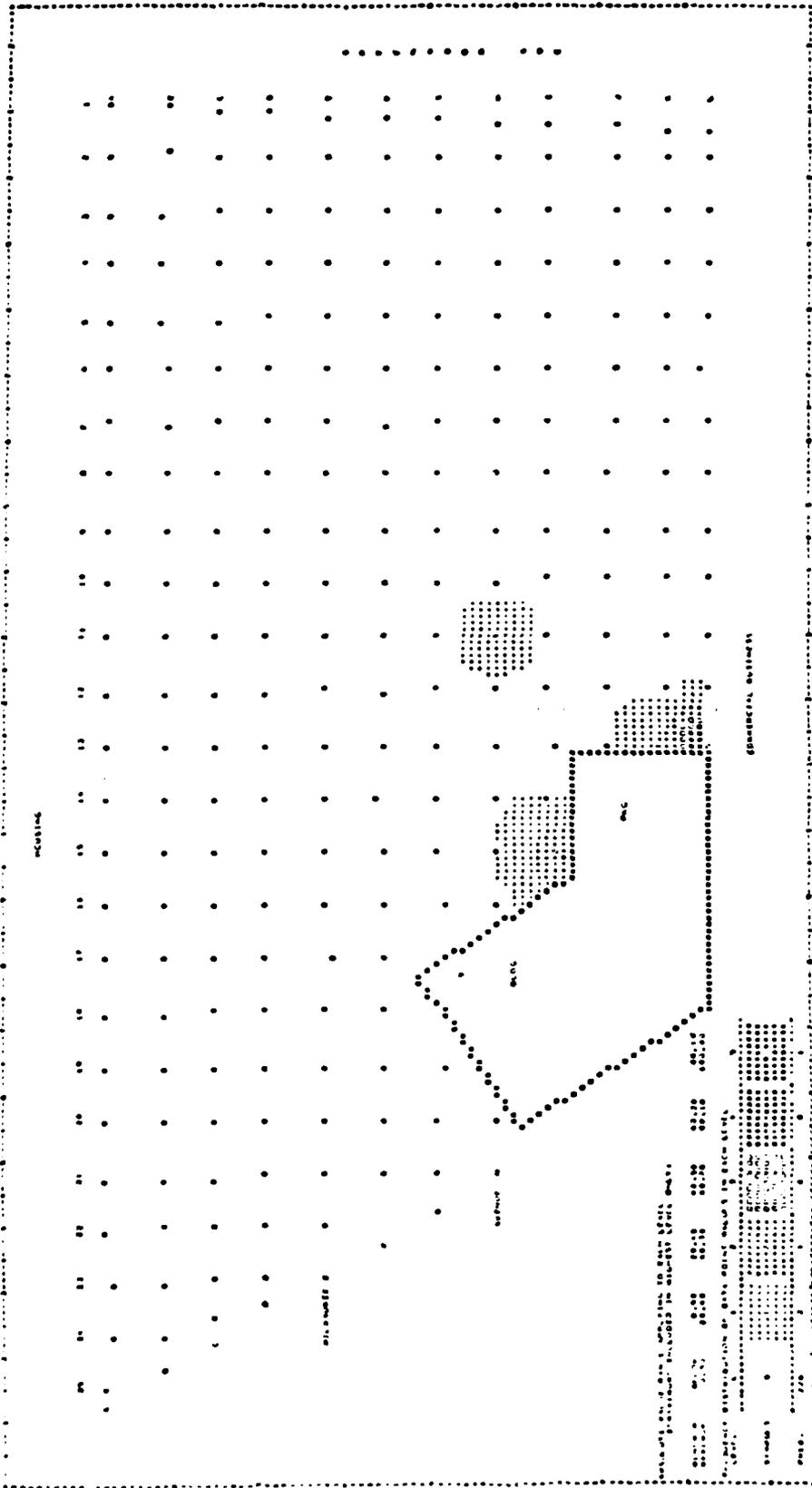
Figure 4. Reed-canary grass (Phalaris arundinacea L.), is a persistent weed that is difficult to eradicate once established. Cover importance and distributions of the plant are consequently monitored closely. Selective management against this plant is facilitated by this map which shows areas of greatest establishment.
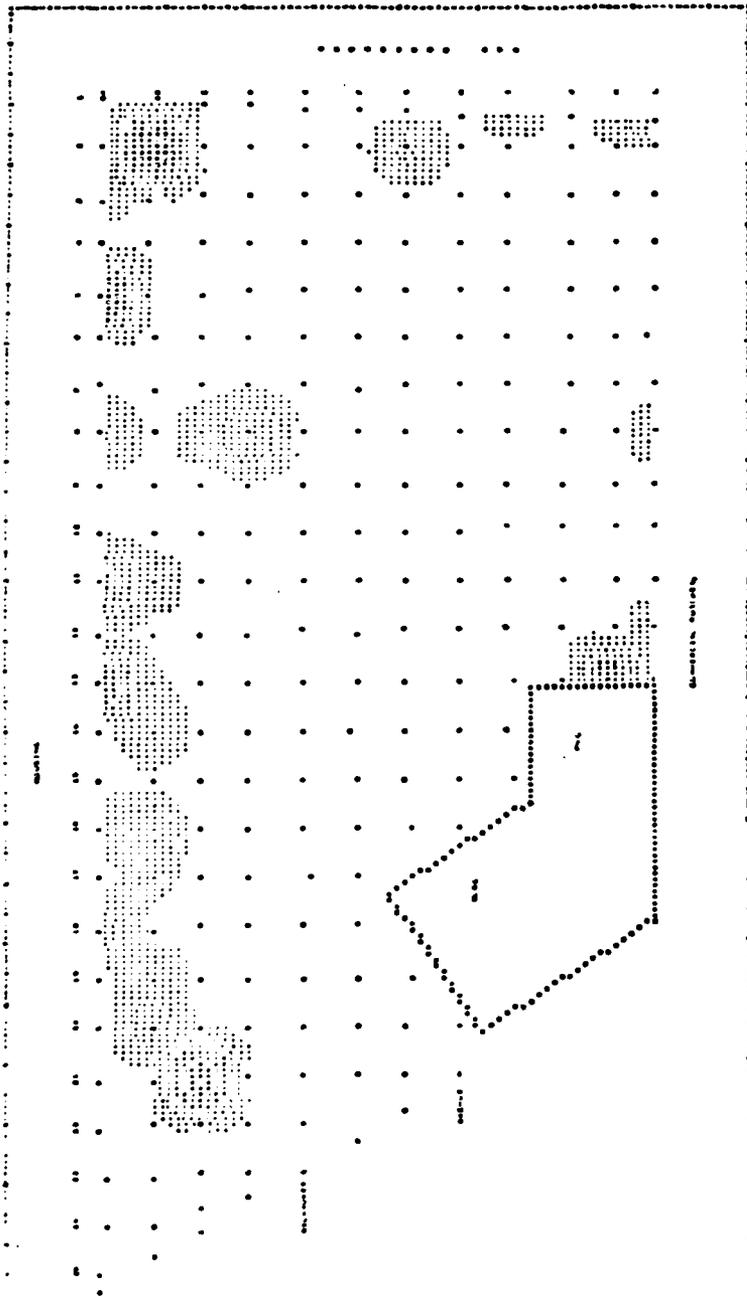
Figure 5. Some native-weed species such as sunflower (Helianthus grosseserratus Martens) can become persistent management problems. This map shows this species to associate with disturbance in the Woodworth Prairie. Notably, the areas where this plant has greatest cover are along disturbed fence lines, and associated with the historical go-cart track at the east end of the parking lot. Other localizations co-occur with historical vehicular intrusions in the preserve. This is a 10-level symap.

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Table 1.   Computational output is used with graphics to monitor vegetation dynamics and the effects of management and non-management on natural processes in the Woodworth Preserve. Plant cover and frequency values are a few of the indices used in this work.
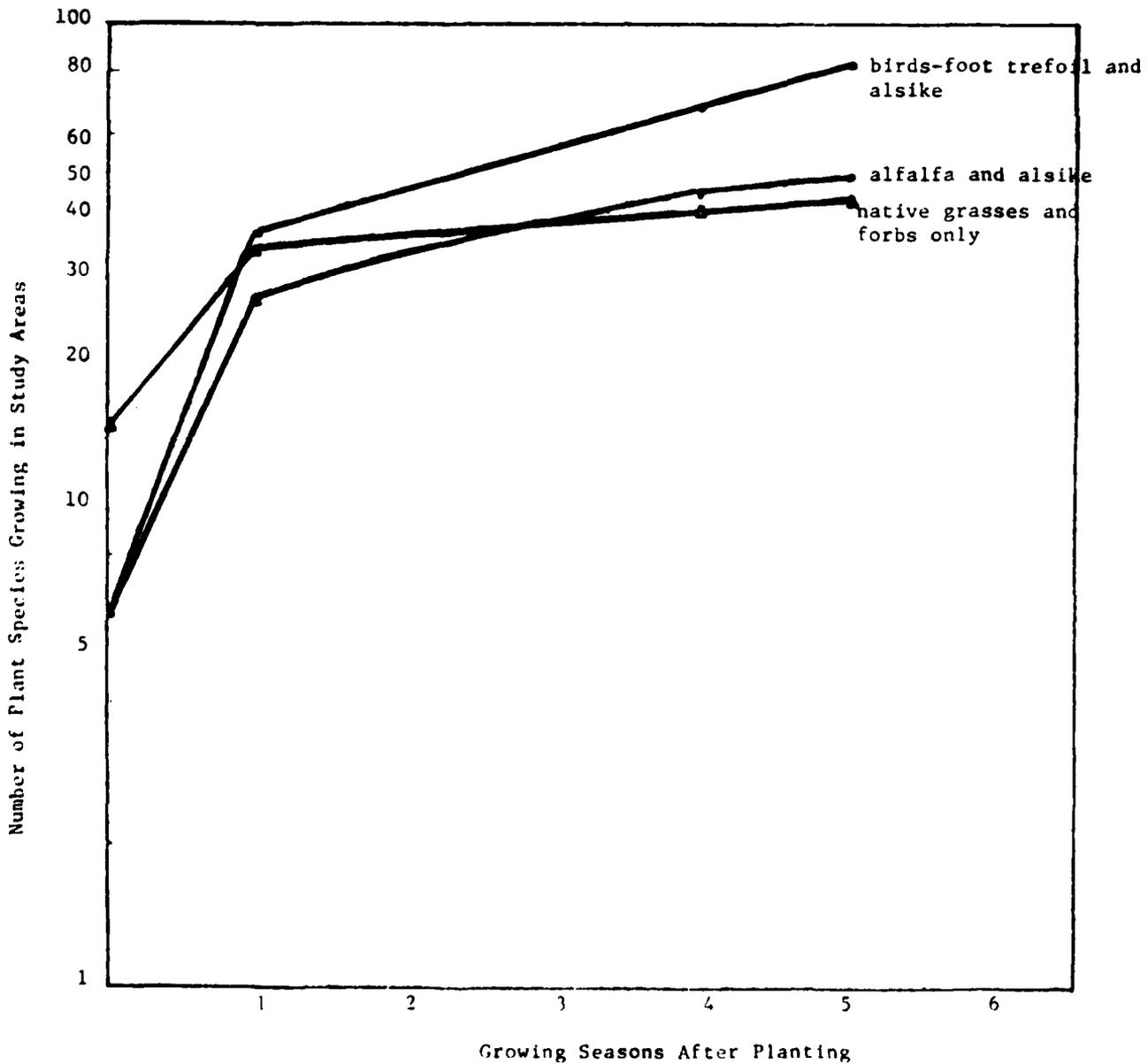
Figure 6. Results of the 1977 planting of native species and two agronomic mixtures on Dump 2 at Jackson County Iron Company.

APPLICATION OF FISH GUILDS IN ENVIRONMENTAL ASSESSMENT

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We have worked with the Construction Engineering Research Laboratory in terms of an ecological grouping of fish species to help assess various kinds of environmental perturbations. Typically, impact assessments are done on a species-by-species basis. We often determine which species are present in an area. Most often, we put these species in a list, taxonomically arranged and then look at the impact on each species. What this really means, of course, is not looking at each species, but rather at fishes or birds.

In Oklahoma, several hundred species could potentially occur at any one site. What we do is very general. We don't have enough information on all the species, and we can't possibly spend the time to deal on a species-by-species basis. We put those lists in there, but in fact, touched relatively few of the species. However, I don't want to imply that making species lists is unimportant; reviewing what we think is there is important. If we just concentrate on the very common species (the top 20 or 30), there may be some very important impacts on a number of other species. In fact, we know that quite often, rare species that we would not have thought about are affected. So even if it's a relatively short-term, broad analysis, I think that we should at least have thought about each species that could be present and see if we have any knowledge of possible impacts on them. However, I do think that we could help ourselves in terms of channelizing our thinking around more ecological lines; in summarizing data, it would help to divide these species into classes consisting of forms that were similarly affected by a given habitat alteration.

That single step of rearranging such a list could be helpful in conducting assessments and identifying species that could be similarly affected by a particular environmental perturbation. We have devised a relatively simple ecological classification for freshwater fish species. We have done it in a very general context with the idea that it could form the basis for a classification which could be used in nearly any of the 48 conterminous states.

Despite geographic variations and a number of other considerations, a very general classification system could facilitate work in any one of these areas on a particular site or tract. We have attempted to put in features that could be evaluated on most sites in terms of freshwater species. While we rely on the value of the guild concept, the categories we identify are not guilds in the strict sense of Root's definition. Some of the variables used

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to characterize the species are not exploitable resources. Thus, we're not using guilding in its pure sense, and I don't think I would apply guilds to the kinds of things we're doing. What we really have done is develop some sort of a general ecological classification for these species.

I will briefly go over what we propose as a sort of general classification and its general framework. In water body morphology, we have divided the species according to whether they are considered estuarine; large rivers and lakes; medium-sized streams; headwaters, springs, and mountain streams. Thus, we have four very broad categories. We've arbitrarily differentiated among the stream types in terms of some of the examples, with large rivers being about 50 meters across, flowing throughout their length and medium-sized rivers (again, an operational definition), less than 50 meters across, commonly broken into a series of flowing areas. They include ripples, rapids, then pools, and headwaters less than 5 meters across which may be intermittent. The mountain streams, particular mountain streams, might have a morphology of either a medium-sized stream or headwater, but their waters are typically cool and highly oxygenated. A species is listed under the water body type it most often frequents; of course, many species are found in more than one of these categories, and you could place species in more than one category, depending on the size and diversity of the area being evaluated.

We have looked at current from the standpoint of whether the species requires something it provides, such as a hard substrate or highly oxygenated water. These species may be able to live in an area without current, but typically, they thrive only in areas characterized by moving water. Wave-swept beaches may satisfy this moving water requirement for some forms, and species rarely found in lakes and ponds are assumed to require current; in other words, this was in terms of our operational type of definition of attempting to assess the situations. These were not high-budget types of operations, where we would do extensive surveying over a number of years, but sort of "armchairing" things after we had species lists derived and then doing some kinds of collecting.

Now in turbidity, we talked about whether it was tolerated; here, we're talking about whether the species exists in areas of long-term turbidity for, say, more than a few weeks. In the case of us attempting to operationalize this, we took a rather extreme definition of turbid waters. We generally considered nontolerant species to be those that are never found in those areas where we have long-term turbidity.

When we refer to structure, we're talking about whether it is preferred, and here, we're saying that species are found in association with macrophytes, submerged logs, artificial reefs, and similar things. Species considered not to prefer structure, or those rarely found near structure, are found equally often near or away from the structure. In substrate, we divided species into those preferring rock bottoms or sand, or those not demonstrating such preference; for some of the examples, we couldn't decide. Species not showing preference would be those that are found under different substrate types; we also put those that were found over a number of different substrate types in that third category. That would also be the same category--an additional catch-all area--where we put silver mudbottoms.

For food categories, we looked at those that ate invertebrate prey, fish, and detritus. We placed omnivorous fish in a fourth category. By invertebrates, we mean macro invertebrates and species like crayfish, benthic invertebrates, zooplankton, species with filter-feeding young, and some non-feeding adults, such as the non-parasitic lampreys. We also considered the fish-eating fish in this category, since they eat invertebrates during some stage of their life cycle. We also put parasitic lampreys in the fish category. The detritus category assumes more than just detritus in the diet; it includes algae, paraphyton, sediment, and it really characterizes detritivores and herbivores. Only one North American herbivore--the grass carp--normally eats macrophytes, so we included it in this category, rather than create a separate subdivision. Omnivorous forms obviously eat food that is included in more than one of these other categories.

What we're putting together is a series of value judgments, so some flexibility is required. With this kind of a classification, anyone with any facility for computers could stick this thing together, put a matrix in, find out the area, get the species, print it out, turn in the assessment report, and collect the fee. However, I think anyone who knows anything about this fully understands that this is not the case at all. It takes a good naturalist, someone with knowledge about many of these fishes to want to place them reasonably in these kinds of categories and then interpret the effects on them. This is a very simple initial system, and I think we should consider it as that. We do not use this in place of a trained biologist. We use it to help him or her organize information and then present it to others in groupings that might be helpful.

In breeding sites, we included river channels, gravel shoals and ripples, structure, nests, and those species that broadcast their eggs randomly. River channel forms require flowing water to spawn successfully. The eggs usually roll over the bottom or drift in the river channel. Gravel shoal and ripple spawners include forms such as salmon as well as species that live in shoals and ripples. Eggs of these forms usually require highly oxygenated silt-free water to hatch. Nesting forms include those that actively construct some sort of nest. Species requiring structure to spawn are those that spawn in vegetation, on sticks, or in crevices. This category also includes species such as the stickleback, that build nests out of structure. The eggs broadcast category includes species that broadcast eggs randomly over a variety of substrates. We've taken water body morphology, current turbidity structure, and substrate food, and just put it in dendromatic form; we would expect that for any particular situation, any specific site where one is doing an assessment, there would clearly be a much smaller number of categories than this overall dendrogram would hold. A particular species might be represented for some of these, but none for others. Categories might sometimes prove to be unimportant or irrelevant, and obviously could be removed.

The hierarchical arrangement is not thought to be particularly important in terms of whether current or turbidity is put first. In some places, a current was required. We didn't have any species that really tolerated turbidity, so some categories dropped out, but the arrangement could vary. Typically, what we did was place the ones having two-state kinds of characteristics toward the trunk end of the dendrogram and put the others over on the other side; however, they could be arranged in a variety of ways.

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When we first approached this problem, the first approach of somebody like myself--a numerical taxonomist--was to look at a series of different kinds of sophisticated clustering routines and a number of such representations. We wanted to get nice clusters and then go from there. Again, we are talking about fuzzy clusters, at best, and generalizing in any kind of broad context is almost impossible. Because of geographic variation in requirements resulting from differences in season and differences in terms of adults versus immatures, there are many problems. Again, except in only the best-studied sites, there will be information on only relatively few of the species.

In many of the sites that we typically would be working, there are a number of species about which we have some information. For example, while gathering samples, we might find a number of minnows, and virtually nothing is known about the ones typically found in Oklahoma. In such a case, we would rely rather heavily on the naturalist's perspective. They're found in association with other fishes that are well known, so we would place our best estimate that those are the species they should be associated with. Sometimes we may guess wrong. I think we can all say that more research is needed to understand all that we can about the specific requirements of individual species. We should also be very cognizant of the ongoing operation and ongoing decisions. Next, we will provide a couple of examples, and I might point out that they are not necessarily typical examples. Typically what we would do is to predict which of those categories would be influenced in a relatively undisturbed area. For instance, if we're going to increase turbidity, we would particularly try to highlight those species that are affected by that disturbance.

The first example involves the species of the Red River and Lake Texoma and the Red River between Texas and Oklahoma. We compiled a listing of all the species ever collected in these areas. We then classified them according to what we knew of their biology in terms of the variables, using information that we knew, had collected, and obtained from the literature. Other literature on these species contains much information on which species are found in current, which are found in turbid water, etc. To begin with, we're obviously in a large rivers and lakes subdivision. The Red River is a large river for Oklahoma, and Texoma is a large lake, so this is the part of the dendromatic classification that we used.

One fish species that I classified was Hybopsis estivalis, or speckled chub. It requires current, and is not found in still water, lakes, and ponds. Notice that turbidity, preferred or not preferred, tolerated or not tolerated, does not enter into this. All of the species found in the Red River can tolerate turbidity. Again, most of the species that require current did not necessarily require structure. It is not preferred and not required. Thus, Hybopsis estivalis fits in this category. It eats invertebrates. Although we do not know about its reproduction, our best guess is that it is a channel spawner; some other forms related to it tend to be.

The bluegill--another species that was found in the Red River--does not require current, and, in fact, is adverse to current. It is more abundant in still water and prefers structure. It is also more abundant where there is some sort of cover, such as vegetation. It eats invertebrates and spawns on a nest. This is the way to classify these species, using your own experience

and that of other ichthyologists. We ended up with a reduced classification, since a number of categories had no species present in the Red River.

The fish that require current are excluded from Lake Texoma. This may seem trivial, but it is the kind of thing that might be asked in an impact assessment. In fact, most of these species were excluded from the river. There's a listing of species involved. The only species present now in the lake in any kind of number at all are the Notropus potteri, the chub shiner, and Percino caprodos, the logperch, and they are found on the wave-swept beaches. The other species are all gone.

This example shows that such a classification gives us an idea of which species would be excluded. It also offers us somewhat of a prediction for Lake Texoma. There have been some impoundments proposed upstream in the tributaries--at least one of the tributaries of Lake Texoma. We would guess that species that spawn on upstream shoals would be blocked from reaching those shoals. And you might expect a population decrease of white bass and striped bass, which are now abundant in the lake, having major spawning runs up both rivers. Again, here is a prediction we can make. This is a broad, sandy river much like the Red River, and turbid again. Some other species are the speckled chub and the river darter. There is also Alosa chrysochlorus-- the shad found in the river--and Alosa sependisima--the Atlantic shad. Some other characteristic species are the emerald shiner, the ghost shiner, and the bluegill.

The second example involves the channelization of a portion of a medium-sized stream. We collected all the species from both channelized and unchannelized segments. We ended up with a reduced classification, since only four categories were filled. One species--the stone roller--requires current. Another group of other species does not require current, and they were divided into those that prefer or require structure and those that do not. Channelization increases the flow rate and removes obstructions in the stream bed; in other words, it takes out cover. And, in fact, in looking at the species presence we found that the stone roller (the current-requiring form) is found in the channelized portion but not the other. The forms not requiring structure were more abundant in the channelized portion. Species that do not like current and require structure were more abundant in the unchannelized portion. The one big exception was Gambusia affinis, which was very abundant in the channelized portion; however, it was proliferating in small pools by the edge of the channelized stream.

We feel that this classification offers at least insight into species biology and possibly some predictive value.

We were also asked to look at creating a similar type of classification using various water chemistry parameters. Here, we tried to define chemical parameters of importance to fresh water fishes, and then organize species into groups reflecting similar requirements or tolerances for these parameters. We evaluated oxygen level, pH, salinity, alkalinity, total dissolved solids, carbonate level, and ammonia level. Again, we threw out a number of other types of characteristics that we felt were not particularly useful. It wasn't likely that people would have knowledge of them or they were unmeasurable in one way or another. But what we found here was that in the chemical work, there were a number of very serious problems. For instance, when we tried to

look at chemical optimums for various species, we found that they cannot be used, because in some ways, many of them were very similar over most of the freshwater species. For example, if a lot of oxygen is introduced, and various kinds of preference tests are performed, the species would go to the more highly oxygenated areas. There are very few areas, very few kinds of things, where you would find very low or high saturation of oxygen; most species preferred a "middle ground" in terms of the optimum, or preference, if other conditions were kept equal. Then, realistically, we should focus on tolerances for chemical conditions. While a fair amount of tolerance work has been done, it has been done on relatively few species, and there is a dearth of information for most North American fishes. Thus, for any realistic sample for most sites, very little information is available on preference for pH, and so forth. It is likely that for any particular example, even a very simple example, there would be very little data. However, the most bothersome aspect was that the arbitrary divisions did not in any way reflect the complexity of interaction between physiological tolerances and environmental conditions. We are all aware of the interactions of CO_2 and oxygen, temperature, and pH and how those relate to fish restoration. A simplistic kind of classification such as the one we're discussing here really obscures these kinds of relationships. Also, we weren't dealing here with resources that are similarly exploited by a group of species. We're talking about chemical conditions, so I think that attempting to look at chemical tolerances or chemical kinds of parameters in a similar way for any broad application is probably unrealistic at this time.

Returning to the physical parameters and this particular type of classification arrangement, we think that it can be helpful in assessing ecological impacts on species in that it tends to group species that share functional relationships in the environment. Using the classifications can lead an investigator a step beyond a species-by-species type of analysis of environmental impacts and emphasize criteria that are of importance for determining at least the number of species involved and where they might fit. Furthermore, it will help us check other, less common species to help us make intelligent choices. One of the other advantages it provides is that the classification process points out where your weaknesses are in terms of knowledge--that because of the particular impacts, certain parameters require further study. Certain experiments or sampling schemes may have to be devised to determine where these species are found and how they're associated. For example, such a classification would enable us to organize fishes into categories and would help pinpoint which species are likely to decrease or increase. This would make us much more accountable for our predictions. We think that putting it in tree form allows easy retrieval, helps present the information, and keeps it relatively simple. I think this kind of a classification can be modified easily to suit a specific problem, although there may be some other kinds of subdivisions that are needed in a particular case. We set it up initially for surveying the fishes of Missouri, for which ther is a fair amount of information. We also took into account fishes that we had in Oklahoma and added some obvious ones for species like salmon. But then we took the overall general scheme and attempted to apply it to the fishes of Utah, and it's not really designed for that. I want to emphasize that. I think that what we were thinking about were things like modifying a particular area which is describable in one way or another. By this we mean individual projects. But we thought in terms of making it general enough to apply to broad faunas, such as those for a state. For the Utah project, we

had to add a couple of other categories. We've now looked at about 200 species out of the 700 plus known in the conterminous United States, so a few would be added. On the other hand, there should not be too many additions. We don't claim to have solved any decision-making problems or to have replaced what is needed in terms of sound biological knowledge of sound interpretation. However, I think that if we were to get a number of assessments, just making the step of using ecological rather than taxonomic kinds of classifications and using that as a format within which to present their data, would go a long way in terms of focusing on the relevant problems and ideas for assessing impacts.

SESSION IV: SOME POTENTIAL APPLICATIONS OF GUILD THEORY

INTRODUCTION

James R. Karr, Moderator, Department of Ecology,
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The purpose of this session was to explore some potential applications of
the guild concept that are currently being examined by various research
organizations.

Dr. Karr's comments during the workshop dealt with the importance of
defining terms used in management and research so as to allow a thorough
understanding of the concepts being employed - whether one calls it "Gouda
cheese, guilds, rabbits, or elephants" is irrelevant as long as their meaning
is adequately explained.

GUILD-BASED LAND MANAGEMENT MODEL

William D. Severinghaus, U.S. Army Construction Engineering
Research Laboratory, Champaign, Illinois*

Background

Objective

The objective of this paper is to: (1) define the goals of the
USA-CERL's guild-based research program; (2) present a developmental plan for
review during the early stages of development and formulate a definitive plan;
(3) identify specific research initiatives that will require satisfactory
completion to satisfy the overall goals; and (4) describe a guild-based land
management model.

Project Objective

The objective of this project was to develop a means to help Civil Works
project managers and recreation area managers (1) rapidly assess the changing
condition of their areas; (2) determine along a gradient, which identifies
conditions necessary for various natural resources management goals, where a
specific parcel of land might fall; (3) be able to predict the pre- and post-
project direction of change, negatively or positively, and how this relates to
changes in plant and animal populations; (4) determine if there are available
procedures to upgrade the condition of the specified area, how quickly the
procedures will return the area to a desired goal, and cost per unit area.
This computer-assisted procedure can then be used to project maintenance costs
in future years, make decisions as to where maintenance funds might best be
spent, and project how much of an effect a project might have on the
environment for inclusion in environmental assessments and for pre-project
planning.

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*See the article in Appendix A entitled "Appreciation of the Guild Concept to
Environmental Impact Analysis of Terrestrial Vegetation," by Robert A.
Johnson. The Article appeared in the Journal of Environmental Management,
Vol. 13 (1981), pp 205-222 and is reprinted with permission. Also see the
articles "Guild Theory Development as a Mechanism for Assessing Environmental
Impact" by W.D. Severinghaus and "Effects of Tracked Vehicle Activity on Bird
Populations" by W.D. Severinghaus and M.C. Severinghaus. These articles are
in Environmental Management, Vol. 5, No. 3, (1981), pp 187-190 and Vol. 6, No.
2 (1982), pp 163-169, respectively.

Approach

The complete development of this program, with all of the various pieces, will be accomplished in different phases.

Phase I is the concept development plan which details all parts of the project. This report is designed to respond to this goal. It is the critical review of this plan that will determine the final direction of the program.

Phase II is the analysis of the cause-and-effect relationships between Civil Works project activities and the environment. It is from this phase that rates and direction of change will be determined and the predictive algorithms developed. The predictive abilities of this system will essentially be accomplished by applying to guild theory this cause/effect data. The application of the guild concepts to such analyses is underway.[1,2,3]

Phase III involves first the examination of those techniques, plant species, and propagation procedures that are suitable for use. Although an extensive body of literature has been produced by many organizations (Argonne National Laboratory, Soil Conservation Service, USDA Forest Service, WES, Bureau of Land Management, Department of Energy, and numerous state agencies and universities), most of this information focuses on reclamation practices where the last stage is characterized by permitting the land to rest for long periods of time (from 5 to 100 years, but commonly 10 to 20 years). A second part of Phase III will be to develop a reclamation program that will be more compatible with the post-project need to usefully and aesthetically reclaim the land. The third part of this phase will be to monitor each method's effectiveness and cost per unit area to allow incorporation of such data into the overall system.

The development of a system that will house all of the acquired information and make the information available to users is Phase IV. The system is proposed to be computer-based and will use as a base the guild concept and algorithms developed from guild signatures. The inputs to the system will be variable and dependent on the degree of resolution desired by the user. The simplest, least expensive level will also yield the lowest resolution while the most complex, expensive level will yield the greatest resolution. The input possibilities will be: (1) aerial photograph or LANDSAT data tape analysis; (2) on-site vegetative/soil disturbance transects with a calculated index; or (3) a transect which would quantify the density, diversity, and biomass of birds for use in guild analyses. Outputs of the system will be various information on the condition of the area; its suitability for various types of land management goals (wildlife management, recreation, etc.); its rate of change (by comparing with previous samples); potential methods to upgrade areas in poor condition, rate of recovery, and relative cost per unit area.

Scope

Initially this project is being developed for areas in the Midwest with research efforts directed at Lake Shelbyville. Other general ecological zones may be incorporated as their basic phases are completed.

Research Initiatives

In the field of land reclamation, there is no method by which planning for and implementation of reclamation procedures can be accomplished without expensive, highly technical site studies. A program of this magnitude has been avoided by most research institutions with claims that the environment is far too complex to be able to accurately predict which reclamation procedures best fit a specific situation.

To accomplish this project, several research initiatives must be taken.

1. LANDSAT data tapes or other aerial photographic materials will have to be researched to determine if land quality can be ascertained and if predictive trends can be determined by examining historic tapes.

2. Can the land quality values from the aerial photographs be correlated to the Vegetative/Soil Surface Disturbance Index, to the Emlen bird transects, and to actual conditions at a sufficient level of significance ($r^2 \geq .70$)?

3. Can guild signature curve analysis, principal component analysis, and/or discriminant function analysis be used to analyze land quality through use of guild theory? Can this then be used to accurately determine the missing environmental attributes, and predict the future magnitude and direction of land quality?

4. Maintenance procedures must be tested to determine effectiveness under various levels of use and their relative costs.

5. Manipulation of construction scheduling and effective/wise land use planning must be accomplished to allow maintenance procedures to be compatible with long-term management goals.

User Needs

The Environmental Advisory Board met in Denver, CO, in August 1982. Representatives from the Department of the Interior, OCE, USA-CERL, COE District and Division offices, WES, and other organizations discussed needs for habitat evaluation methodologies applicable to Civil Works project planning. This program is designed to help evaluate and predict results of construction activities for waterways development projects.

Other products that may apply to planning problems are presently available or readily developable or modifiable at USA-CERL (Point of Contact: R. E. Riggins, Environmental Program Manager, USA-CERL, Comm. 217-352-6511, ext. 234 or FTS 958-7234).

Analysis Inputs

Introduction

Overall inputs must meet two basic criteria: (1) they must be reasonably simple/inexpensive to obtain; and (2) they must supply sufficient information to accurately depict the actual conditions on the site or training area. The data used must be statistically validated.

The inputs will be of several different types and will depend on the availability of funds, the user's purpose for accessing the system, and the confidence limits the user wishes to obtain. The two basic categories are background inputs and transect inputs. The background input will deal with a gross overview of the ecological conditions to allow the system to select the appropriate package of algorithms. The transect inputs will vary from LANDSAT data tape or aerial photograph analyses which are relatively inexpensive and cover broad expanses of land, but also have the lowest resolution to on-the-ground (foot) surveyed disturbance transects which will require a generally low level of technical ability, be of moderate expense, and reduce the margin of error, to bird census transects, which will require an onsite visit by an ornithologist; this renders the method more expensive, but yields much more precise information.

Background Inputs

A number of inputs will have to be used to prepare the system for analyses within the appropriate ecological zone. Once the zone is identified, a number of zone-specific "filter" questions must be answered. These filter questions are designed to more tightly define some of the major variations that exist within an ecological zone. An example of inputs are as follows:

Ecological Zone: humid grassland
Average Rainfall: 34.3 inches
Season of Rainfall: April to September
Distribution of Rainfall: Short storms
Mean Temperature: 49.1°F
Soil Characteristic: Upland clayey
Elevation: 1000 to 2000 feet

This information will be needed to help determine what type of refurbishing procedures should be implemented. An area with multiple input requirements due to complex ecology may have to be input for each major variant.

Another series of "filter" questions will deal with what the user is requesting as an output. This will require that the user determine what information he/she needs and how it will be used. Accessing the system with different input will not change the analysis, but the time and expense will be reduced by not acquiring more information than is required.

Aerial Photograph or LANDSAT Input

Land quality change is considered to occur as a response to destruction
or construction associated with the variation in use of land. A newly
initiated USA-CERL research program is now addressing the development and
implementation of digital image-processing software to perform land cover
classifications and analyze historical change. From this relative land
quality, assessments can be made that will produce a land quality value that
is statistically correlated with on-the-ground data on habitat change. The
availability of this information as an initial input gives the user a number
of different benefits. The following is a list of considerations:

o LANDSAT data are easily and inexpensively obtainable.

o The user can observe changes with time by obtaining data tapes from
  earlier years.

o An overview of the project area can be made with areas of specific
  concern being identified.

o Continuity from year to year can be maintained without on-the-ground
  verification. This becomes important since voids in the data could
  otherwise result because field studies were not required or funded.

o The area can be viewed in relation to surrounding land condition (at
  one time or as conditions change from year to year).

Foot Transects

Only a low level of resolution can be obtained through the use of LANDSAT
Data Tapes (one pixal = 50 m or 25 m, which is expensive). In many cases,
this may not provide adequate confidence limits in the system's ability to
determine the condition of the area under consideration. This will be
especially true if expensive reclamation procedures are going to be
implemented or if the information is to be used to determine suitability or
location of wildlife food plots or wildlife habitat enhancement.

The foot transects realistically reflect the amount of physical damage
done to the natural conditions area and can be translated to an index of the
disturbance of the vegetation/soil interface. This shall be referred to as:
Vegetation/Soil Surface Disturbance Index (V/SSDI). The V/SSDI is a measure
of the percent of visible damage and is obtained by walking random transects
across an area, recording how many pace intervals included damage, recording
this as a percentage, and then averaging 10 such walked transects. Each
transect should be 100 m, or for simplicity, 100 paces long.

Research into the validity of the V/SSDI index is not yet complete but
the evidence supporting its use is as follows:

o Nature will remove man-made scars at a variable rate, depending on the
  mechanism causing the scar and the area's natural capability to repair
  the damage. This natural capability depends on a complex mixture of
  vegetative colonization, growth potential, and climate. The important
  points to consider are that arid areas take longer to heal naturally,

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humid areas heal fast unless the damage was so severe as to result in excessive erosion, and various project activities cause different types and magnitudes of damage. The underlying principle is: UNTIL THE DAMAGE IS REPAIRED, IT IS MEASURABLE.

o   Nine sites have been studied to date. The results show a 0.97 correlation of V/SSDI to loss in endemic bird species. This value far exceeds the accepted level of significance (0.70) anticipated for ecological studies, and the additional six sites surveyed this year should help formalize the statistical significance.

Emlen Transects

When neither LANDSAT, aerial photograph, or foot transect data can determine with sufficient accuracy the level of land quality, bird transects can be used. Emlen transects are a scientifically accepted and broadly applicable method for assessing bird populations[4,5,6,7] by determining density, diversity, and biomass data. It is this type of information, which can be readily tabulated by guild membership, that will form the background of the data base.

How can birds give an adequate picture of the condition of an area? There is an extensive body of literature successfully using this method, but here are a few obvious advantages:

o   Birds use a three-dimensional niche.

o   Most songbird species are readily identifiable in the field, requiring no lag time for identification and data analysis.

o   Being highly mobile, birds respond immediately to any change in their habitat requirements.

o   The diversity of birds in any one area is greater than for most other vertebrate groups; therefore, their subdivision of the resources is greater (resource partitioning, species packing).

Emlen transects and subsequent guild-based analyses will allow a relatively tight definition of the area's condition. If executed properly, the information can be directly correlated to other wildlife populations giving a very broad application of the system. The Emlen transect procedure is generally accountable for all songbird species and has an undetermined degree of error when censusing species with large home ranges, such as raptors.

Analysis Mechanisms

Introduction

Acquisition of data to develop predictive algorithms may be the first task in this R&D program. Establishing ecological baselines and monitoring land changes and rejuvenation is in the planning stages, although many relationships can be obtained from ongoing Army monitoring. The major task is to determine how the inputs will be analyzed and converted to meaningful

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output. The use of the ecological concept of guilding is presently recognized as having the most potential to become an effective tool to use as the background structure for this type of a system.[16,17,18] Analysis mechanisms for guild-based systems have not been completely and successfully tested, although several efforts have been and continue to be researched. Two potentially powerful analysis mechanisms that are under development are the use of guild signature curves and discriminant function analyses.

Data Base

The data base that will make up this system and the algorithms it houses is being obtained from two research efforts that are going on simultaneously. Predictive studies are gathering data that will eventually allow USA-CERL to predict the magnitude and extent of degradation caused by cross-country tactical vehicle maneuver training exercises. These studies have been conducted at six different Army installations. Other studies done on Civil Works recreation areas (e.g., Lake Shelbyville, IL) could complement the installation ecological monitoring data to assist in the guild integrative and algorithm development process. Additional studies will be added that will predict the rate of recovery for various procedures used in reclamation.

Guild Application

For decades, scientists have been classifying organisms (animal and plant life) into groups based on genetic and evolutionary relationships, on the way they interact within ecosystems (organisms within their environment), communities, and populations, and on what functional role they play within nature. A guild, by simple definition, is "a group of organisms that use similar resources in a similar manner."

Use of the guild concept in environmental analyses will drastically reduce the collection of field data necessary for both preproject planning and ecological and environmental condition studies; it will allow the data gathered to be used both within and between ecosystems, thereby reducing ecosystem variability problems.

Although the resources that set one guild apart from others usually are based on feeding strategies, guilds also are separated by breeding, nesting, and other strategies. Examples are animals that feed on insects living on tree bark (generally restricted to birds, but some lizards and frogs may fall into this guild), and animals that use holes in trees for nesting (generally restricted to some birds and tree squirrels). Theoretically, the guild concept has provided ecologists with a new means to examine the inter-action/competition of animals and plants.

In applying this concept to environmental analysis, we modified the definition above by adding, "Therefore an action that affects a guild in a certain manner will affect all the members of that guild similarly."

Guild Signature

Guild signatures are a way of referring to the density of each guild at one point in time. A guild signature curve reflects what has happened over time, or within this system, and how this has changed. A guild signature can be portrayed as a graph (Figure 1) that shows the total biomass (kilograms per hectare) of all the members of each guild. (We are using 10 guilds in this example, although in actuality the number of guilds in our previous studies varied from 5 to 19. Those guilds with no members present would be included and show a total biomass of zero.

When this information is gathered over time or under changing conditions, guild signature curves are obtained (Figure 2). Each separate guild curve (e.g., 1, 2, 7, or 10) represents the change in the biomass of all the members of a guild. Each guild represents a unique set of resources and a unique function of the resource. Each curve can be represented by an equation. When all the curves are united, a guild signature curve (algorithm) can be developed. The research on algorithms based on the guild signature curve requires finding a mechanism to transpose these algorithms into a meaningful statement of the changes occurring and how to mitigate them if desirable.

Discriminant Function Analysis

Most undisturbed environments are tightly packed with species using every potential resource available. The ecological concepts of "resource partitioning" and "species packing" can be used to explain this situation. Two different methods of computer-based analysis are available: discriminant function and principal components. In essence, these methods portray the full complement of guilds on a set of axes, giving the appearance that the system is full (Figure 3). This figure represents a relatively full, undisturbed, packed environment. If an analysis were performed and one or more voids appear, or the shape and/or size of the guild "areas" changes, then the environmental disturbances could be identified by examining the voids or distortion of the guild character space.

This is another analysis tool that has a good deal of potential but will require further study. The major obstacle will probably be the determination of the axis makeup.

Analysis Results

Much of the output will depend on the purpose for which the user is conducting the analysis. There are a number of obvious uses:

o Directorate of Planning and Training personnel need to know if an area can: withstand a higher level of training; has sufficient vegetation to be realistic, if the vegetation is too dense for proper visibility, or if it is so dense that it inhibits vehicle access.

o Land managers may use the system to determine the overall conditions of the land, determine the conditions of specific parcels, select areas for reclamation work, estimate recovery time and costs, and plan for out-year reclamation funding, based on prediction of degradation.

o Wildlife personnel can use this system to help determine the wildlife
   value of specific areas, select sites for food plots, plan habitat
   management/manipulation programs, and determine restocking programs.

o Environmental personnel may use the system to evaluate land quality
   for assessment purposes, to project the effect of proposed
   construction projects, and to explore possible mitigation procedures.

Levels of Output

Once the background questions have been answered regarding the ecological
location of the area, the user will have to select what class of answer is
desired. This is basically a series of key words for the purpose of the
analysis and will determine how far the analysis will go. These key words are
as follows:

Key Words	Purpose
Wildlife Value	Determine the quality of the habitat in a specific area for maintenance of wildlife population.
Wildlife Future	Predict the direction and magnitude of possible wildlife habitat changes.
Environmental Value	Determine the relative quality of the biological/ecological environment, as it relates to significant life forms, for a specific site.
Environmental Future	Predict the direction and magnitude of specific site changes.
Environmental Mitigation	Generally describe appropriate mitigation procedures that fall within the maintenance procedure program and generally outline their effectiveness.
Land Management (General Quality)	Identify if the quality of various specific parcels of land can be extended to an inventory of the entire site.
Land Management-- Prediction	Based on trend analysis, this will determine the direction and magnitude of land quality changes. Similar to other key word selections but not comprehensive.
Land Management-- Mitigation Procedures	Generally describe appropriate mitigation procedures, their nature, and effectiveness. Will reference technical manuals or other documents that detail each specific maintenance procedure.

Land Management--	Will detail the rate at which various types
Mitigation Prediction	of mitigation will return a specific site to
	the desired management goal. Included in the
	analysis will be levels of continuing use.

Land Management--   Present cost of each possible mitigation
   Mitigation Cost   procedure to assist the user in budget
                           planning.

Aesthetic Quality   Similar to others above, but will describe
                           relative values that can be related to areas
                           in terms of aesthetic goals.

Land Management Scenario

Problem: The project manager is in the process of creating the scheduling and budgeting for a construction project. Several areas within the bounds of the project will be in such poor condition that they will require extensive reclamation. These areas (X, Y, and Z) average 500 acres each and have varying degrees of damage that are below the Excessive Erosion level (Figure 4). In addition, there are several more areas that appear to be approaching this same point in quality. These areas (A, B, C, and D) also vary in degree of damage, and average 500 acres each.

Step 1:

Background Information

     Installation Name: _____
           or
     Ecological Zone: _____
     Average Rainfall: _____
     Season of Rainfall: _____
     Distribution of Rainfall: _____
     Mean Temperature: _____
     Soil Characteristics: _____
     Elevation: _____

Key Words

     Purpose: Land Management

Input Mechanism

     Type: Aerial Photography
     Site Designation(s): A, B, C, D, X, Y, Z
     Evaluation(s) per Site: Z

     Values, A: 5.0, 4.3
     Values, B: 3.3, 3.0
     Values, C: 4.5, 3.0
     Values, D: 2.7, 2.9

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Values, X:  2.0, 2.2
Values, Y:  1.8, 1.7
Values, Z:  1.7, 1.3
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The resulting analysis would graphically portray the conditions of the sites and project their future conditions as shown in Figures 5 and 6. These figures both assume that the current point in time is Time 2 and that the planning and budgeting year of concern is Time 3. The user must now make several observations based on these graphs.

1. Areas A and D do not require immediate reclamation procedures but at the rate A is deteriorating, reclamation will be required within 3 years.

2. Area X is increasing in quality, but the margin of error may be too close for suitability. This may require a foot transect or Emlen transect evaluation to accurately determine reclamation requirements. We will assume a more detailed on-the-ground analysis was completed and eliminate Area X from reclamation consideration.

3. Area B is deteriorating, is approaching the quality level that would require maintenance, and will probably require a more detailed evaluation to predict reclamation requirements. Emlen transects would be run in conjunction with Area X; hypothetically, we will assume that B does require reclamation.

4. Areas C, Y, and Z all require immediate reclamation.

At this point, the project manager can prioritize the areas to be reclaimed as Z, then C, then Y, then B, and add Area A to the program later.

Step 2:

The system will now be <u>accessed</u> to determine which mitigation procedures will be the most effective in bringing each area up to the light erosion threshold in a timely fashion. This analysis would be graphically displayed as in Figure 7. The solid line represents the known post and present condition of Area C. The dashed lines from time 2 (the present) into the out-years indicates the future direction in quality Area C could go under five (I, II, III, IV, and V) different programs. The system would then provide a printout of each method, its managerial constraints, and relative cost.

Method - Brief description of basic reclamation procedures for each program. This would include soil preparation, planting techniques, plant species, fertilization, irrigation, mulching, etc.

Managerial Constraints - Detailed discussion of problems such as logistics of equipment, seasonality of activities, the availability or nonavailability for use, seasonality of use, etc.

Relative Cost Per Acre - present and out-years.

Some obvious decisions may be made by examining the graph (Figure 7). For example, Program I is most likely a continuation of the existing program, and Programs I and II will not be adequate (neither will return the area to the necessary level by time 3).

Step 3:

The system is again accessed to obtain the references (technical manuals, etc.) needed to implement the program(s) finally selected.

Research Requirements

Introduction

This section will define the direction that continued research should take to complete the development of the guild-based land management model.

Three major tasks must be completed: (1) finishing the guild-based analysis mechanism; (2) obtaining field data on typical Civil Works construction activity and developing applicable algorithms; and (3) constructing the integrated guild and management decision system. Much of the research will be conducted concurrently with USA-CERL's training area maintenance and prediction program. This will require only modification of this military program for Civil Works.

Guild-Analysis Mechanism

The use of guild signature curves in conjunction with either principal components analysis or discriminant function analysis has been identified as the direction for this phase. This is the direction by which a similar system is being developed to analyze problems on Army tactical vehicle maneuver lands. The general approach will be similar to that of Barry R. Noon.[11]

Algorithm Development

The research phase will require field data from a Civil Works construction activity. Lake Shelbyville in central Illinois has been selected as the site for this data acquisition, since it will require negligible travel from USA-CERL; the construction was completed in 1970, allowing the land to restabilize; there are recreation areas and controlled wildlife management areas, and the University of Illinois Environment Institute has already conducted some "before and after" surveys.

The prime field research will be to set up a riparian and an upland study transect in three areas. Either the Kaskaskia River or the West Okaw River Fish and Wildlife Management Areas, one of the access/recreation areas, and below the spillway. The data of main importance will be mammal and bird versus plant community structure, although other nonaquatic vertebrates will be censused. Each site will be sampled over a two-week period during each aspect of the year.

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System Integration

Algorithms dealing with the ultimate effects of the Lake Shelbyville project and its relation to birds, mammals, and plant community structure will be integrated into a single predictive system that deals not only with the quantitative relationships of the plants and animals, but also the aesthetics of the project.

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BIOMASS (kg/hectare)

4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5

1 2 3 4 5 6 7 8 9 10

GUILD

Figure 1

BIOMASS (kg/hectare)

4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5

5
9
6
8
4
7
10
2
1
3

TIME OR CHANGING CONDITION

Figure 2

PC/DF I

PC/DF II

Figure 3

INPUT INFORMATION

PHOTOGRAPHIC INTERPRETATION

VEGETATIVE/SOIL SURFACE DISTURBANCE INDEX (VSSDI)

EMLEN'S BIRD TRANSECT

SUITABILITY INDEX

QUALITY OF THE ENVIRONMENT
(AS MEASURED BY MANAGEMENT GOALS)

THREATENED
ENDANGERED
SPECIES

SENSITIVE
SPECIES

WILDLIFE
VALUE

MOST
ENDEMIC
SPECIES

EXCESSIVE
EROSION

TRAINING
REALISM

TIME ⟶
(YEARS)

Figure 4

99

Figure 5

100

Figure 6

Figure 7

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APPLICATION OF GUILD THEORY TO ENVIRONMENTAL PROBLEMS USING FISH AND WILDLIFE HABITAT CLASSIFICATIONS AND DATA BASES

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Introduction

Basic Questions Concerning Animal Guilds

1. What is the animal guild?

   The Institute of Ecology Ecological Glossary (1973 Anon.) avoided the problem by not including the word. The New College Edition of the American Heritage Dictionary of the English Language, 1976, has the following definition: "guild (gild) n. Also gild. 1. An association or corporation of persons of the same trade, pursuits, or interests formed for their mutual aid and protection, the maintenance of standards, or the furtherance of some purpose; especially, in medieval times, a society of merchants or artisans. 2. Ecology. One of four groups of plants having a characteristic mode of existence that involves some dependence upon other plant life: the lianas, epiphytes, saprophytes, and parasites."

If we are guided by the Dictionary for the English Language, use of the word "guild" with animals other than man is incorrect. Knowing that scientists place a great deal of emphasis on originality, we will not be constrained by the Dictionary of the English Language, and therefore we must define what the word means to us as individuals. We found guild defined as: "a group of species that exploits some class of environmental resources in a similar way." Levin, S. A., 1974, Ecosystems Analysis and Production Proceedings of a SIAM - SIMS conference. The bottom line is that we in this workshop are using the word guild in a variety of ways. However, there are some basic areas of agreement:

   Usually we are talking about more than one species of animal in a guild. These animals are compiled into an association, group, or

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guild on the basis of a similar characteristics, i.e., animals with
something in common, such as morphology, taxonomy, biology,
physiology, ecology, or distribution.

2.   How Many Animal Guilds Are There?

We do not know, but we believe there are an infinite number of animal
guilds, depending on user needs and definition of the term.

3.   How Can We Identify the Animal Guilds Most Applicable to COE?

a.   Identify the COE information needs for animal information which will
most likely include the following:

What is there? (animal distribution)

What do they require? (animal habitat relations/association)

How much of what they require is available? (availability of
habitat and value)

Where is it located?

How do animal and habitat respond to land use/land cover changes?

What is COE animal management's goal/objective?

b.   Design or selection of a "procedure" for guilding animals which will
meet these needs. There are a number of procedures available for guilding
animals. For example, the different approaches discussed in this workshop, as
well as different fish and wildlife DBMS which could be used in guilding
(DuBrock, et al., 1981).

4.   Will COE Information Needs Change?

Yes, we think they will be very dynamic, because the COE will address a
variety of planning and assessment situations which will involve many
different animal and habitat combinations and conditions.

5.   Is It Feasible To Consider Using Guilding When There Are Several
Hundred Species of Animals Involved in a Single Project?

Yes, we think it is feasible using current technology, and we will show
you a method of developing and using animal guilds for planning and
assessment. In the remainder of our discussion, we will focus on several
general types of animal guilds developed using a computerized data base from
Pennsylvania, including:

- Animal guilds based on taxonomic classification.

- Animal guilds based on associations with habitat classifications.

- Animal guilds based on distribution.

- Animal guilds based on life requirements.

- Animal guilds based on non-biological characteristics.

- Animal guilds based on the National Wetland Classification.

The Pennsylvania Fish and Wildlife Data Base

The Pennsylvania Fish and Wildlife Data Base was developed by the U.S. Fish and Wildlife Service, in cooperation with the Pennsylvania Game Commission, as a pilot project to test and evaluate the feasibility of summarizing existing fish and wildlife information in a standard, consistent format on a statewide basis. The methodology to summarize fish and wildlife species information was called "A Procedure for Describing Fish and Wildlife" (Mason, et al., 1979), or simply, the "Procedure."

The "Procedure" methodology evolved over several years through an extensive information needs assessment, involving meetings with Federal and State agencies, industry, universities, and private conservation groups (Cushwa, et al., 1980). Interim methods that were developed, evaluated, and revised, ultimately resulting in the "Procedure" methodology, include RUN WILD EAST (Cushwa, et al., 1978) and FAUNA (Mason, et al., 1979).

The "Procedure" provides a format for developing a standard species description, structured for computer entry, using the following categories of information: taxonomy, distribution, legal status/use, species origin, population descriptors, habitat associations, food habits, niche requirements, management practices, and references. Species descriptions are compiled from existing scientific literature; standard, consistent definitions and terminology are ensured by the coding instructions and 25 reference appendices. The species description booklet and instructions are designed to permit coding information for both vertebrates and invertebrates, including amphibians, reptiles, fish, birds, mammals, molluscs, crustaceans, and terrestrial and aquatic invertebrates.

All data categories in the "Procedure" are standardized, e.g., species names are specified by standard taxonomic references included as appendices to the coding instructions. Standard, widely accepted classifications are used for associating species with habitat. Each entry is based on actual research, field studies, field notes, or other valuable expert knowledge and is so referenced in the Data Base. The Data Base was not designed to replace biological field studies, but to provide supplementary information to complement site-specific studies.

The Data Base contains information on 844 resident and common migrant fish and wildlife species occurring in the State. The species are distributed among 11 major animal groups as follows:

Group	No. of Species
Amphibians	38
Reptiles	41
Fish	184
Birds	250
Mammals	65
Crustaceans	4
Molluscs	69
Aquatic Insects	90
Other Aquatic Invertebrates	3
Terrestrial Insects	92
Other Terrestrial Invertebrates	8
Total	844

A majority of vertebrate species and a select group of "important" invertebrate species are included. Invertebrate species were included if endangered or threatened, indicators of environmental conditions, or of economic significance.

The information in the Data Base was compiled and summarized in individual Species Description Booklets by six recognized authorities. The Species Description Booklets were checked to assure that each data entry was referenced using published reports, field notes, or verifiable expert opinion. All species descriptions were edited and verified for consistency with the coding instructions and entered into the Data Base. The quantity and quality of data included for each species was constrained by FWS in three ways: (1) categories of information included in the species description booklet; (2) the amount of money given one contractor to complete a booklet ($60.00/species); and (3) the amount of time to complete data collection (less than 1 year).

There are 125 fields of information for each of the 844 species. Eighty-nine of the 125 fields are searchable using the data base management system MANAGE (Wilcott, 1981). The remaining 36 fields can be printed or scanned for any or all of the species in the data base; however, these fields cannot be used for aggregating species having common data entries (fieldname values). Boolean (set) logic can be used to retrieve species information using any or all of the 89 searchable fields.

Animal Guilds Based on Taxonomy

All guilds in the remainder of this paper were developed by a biologist using a remote terminal to interact with the data base. Guilds can be developed based on any single or combination of categories of information in the data base for the 844 species. For example, the 844 animals in the data base can be grouped into several taxonomic guilds, including:

5 phyla	251 families
15 classes	548 genera
73 orders	844 species, 746 of which have common names

In addition, we combined the taxonomic groups into the following 11 guilds for the 844 species:

Name	No. of Species
Amphibians	38
Birds	250
Fishes	184
Mammals	65
Reptiles	41
Crustaceans	4
Molluscs	69
Aquatic Insects	90
Terrestrial Insects	93
Other Aquatic Inverte.	3
Other Terrestrial Inverte.	8
Total	844

We will use these 11 guilds to demonstrate how to associate these groups of animals with other habitat, biological, and non-biological parameters, i.e., the process of guilding animals with selected parameters.

Animal Guilds Based on Habitat Classifications

The first step in guilding animals and habitat classifications is to review the effectiveness of several different general fish and wildlife habitat classifications in sorting/guilding animals into homogeneous units based on animal presence or absence. We are looking for a classification which includes strata that relate to "animal communities." These communities include vertebrates and invertebrates which use terrestrial and/or aquatic environments to complete their life cycles. This classification should be a spatial rather than a point classification, since animals usually occupy a geographic area in going about their day-to-day activities. The classification should contain strata that are nested or hierarchical. This is needed in order to address animal communities which include species such as field mice that use a relatively small area to complete their life cycles, as well as species which are migratory and may move across a continent seasonally. A final requirement for our classification is that it be mappable, and preferably that it already be mapped.

In the United States, we do not have a national fish and wildlife classification or inventory. We use classifications, inventories, and maps designed for other resources as surrogates for fish and wildlife habitat. The Fish and Wildlife Service is conducting a study to help determine which of the existing classifications partition variations in fish and wildlife resource (populations and habitats) into more homogeneous units. We will use some of the basic methods developed in this project to guild animals and to make a cursory examination of several national surrogate habitat classifications.

It is important to stress that none of the classifications to be used in this section were designed as a fish and wildlife habitat classification. Each of them has and is being used as a surrogate, primarily because it is all that is available, and fish and wildlife agencies have not had sufficient funds to develop a classification or inventory of fish and wildlife habitat.

Guilding on the Basis of General Habitat Association

The 844 animals were sorted into guilds on the basis of their general habitat association. Forty-nine percent of the animals were listed as aquatic, 12 percent as riparian, and 44 percent as terrestrial. Some of the amphibians were listed in all three guilds (Table 1).

USGS Land Use and Cover (LU/LC) Classification

Animals were associated with one or more of the 46 level II land use and land cover classes identified by USGS (Circ. 964 - Anderson, et al., 1976). These associations were made on the basis of a description of the LU/LC classifications and habitat requirements of the species. No map of LU/LC classes was available to the experts compiling the animal data. For presentation of the data, we included six level I LU/LC classes (Table 1), and the guilds of animals by group associated with each LU/LC class. The 844 animals were grouped into six LU/LC classes; we found 3 percent associated with barren land and 55 percent with water (Table 1).

Potential Natural Vegetation

Kuchler's 1964 classification of the potential natural vegetation of the United States (PNV) has been widely used by resource people. It was used by the Forest Service in 1975 and 1979 for Resource Planning Act National Assessments. It was also used by the Bureau of Land Management in their Federal Land Management Planning Act inventories in the West. Bailey (1976) also used it as one stratum in his classification of ecoregions of the United States. There are five major classes of PNVs in Pennsylvania (Table 2). Fifty-two percent of the animals were associated with Birch-Maple, 51 percent with Mixed Mesophytic, 60 percent with Appalachian Oak, 58 percent with Northern Hardwoods, and 51 percent with Oak-Hickory-Pine.

The Society of American Foresters (SAF) Forest Cover Types

Sixty-one Society of American Foresters forest cover types have been identified in Pennsylvania. We combined these into nine forest type groups for demonstration purposes. We can guild the animals on the basis of the 61 SAF types (Table 3) and/or the nine type groups. Animals were classified on the basis of their association with an SAF type. No map of the type was available to the experts compiling the data. Therefore, animals were associated with forest types or forest type groups by a description of each type and knowledge of the animals' habitat requirements or use.

Ecoregions

Bailey's 1976 classification of ecoregions of the United States was used to guild animals. Studies are currently underway to evaluate the effectiveness of different land (including terrestrial and aquatic environments) classifications in partitioning animals' characteristics such as occurrence, density, etc., into homogeneous units (Inkling and Anderson, 1982; Anderson, et al., 1982). Ecoregions of the United States is one of the classifications being evaluated. This classification is also used as the ecological framework for the National Wetland Inventory (Cowardin, et al., 1979) and therefore of high potential value to people interested in

classifying fish and wildlife habitats. We guilded the animal data by
ecoregions. Pennsylvania is stratified into the Humid Temperate Domain; the
Warm Continental, Hot Continental, and Subtropic Divisions; the Laurentian
Mixed Forest Provinces; and the Northern Hardwood, Mixed Mesophytic, Birch-
Maple, Appalachian Oak, and Southeast Mixed Forest sectons (Table 4). Guilds
of animals associated with the five ecoregion sections were: 80 percent of
the 844 animals were in the Northern Hardwood Forests, 61 percent in the Mixed
Mesophytic, 70 percent in the Birch Maple, 88 percent in the Appalachian Oak,
and 54 percent in the Southwest Mixed Forest (Table 4).

Hydrologic Units

We included an analysis of guilding the 844 animals on the basis of the
Office of Water Quality Data Hydrologic Classification. The following
analysis shows how the 4 (Figure 1) level strata relate to the occurrences of
the 844 animals. We found that 74 percent of the 844 species occurred in the
mid-Atlantic region, 56 percent in the Great Lakes region, and 80 percent in
the Ohio Region. We also sorted the animal data into the 10 subregions (Table
5) and found that 52, 58, 47, and 72 percent of the 844 animals occurred in
the four subregions of the mid-Atlantic region; 47, 55, and 43 percent in the
three subregions of the Great Lakes region; and 72, 61, and 67 percent
occurred in the three subregions of the Ohio region (Figure 1). Data on the
844 animals could have been sorted/guilded into the 14 accounting units and/or
the 56 cataloging units.

Animal Guilds Based on Species Distribution

There are 67 counties in the commonwealth of Pennsylvania. We guilded
the animals based on the percentage of the total number of counties in which a
species was known to occur (Table 6). Thirty-two percent of the 844 animals
occurred in fewer than 10 percent of the 67 counties. All of the counties had
at least 321 species. Each of the 67 counties could represent a guild, and we
found that 37 percent of the counties had between 370 and 399 species, 37
percent had 400 to 424, 12 percent had 425 to 449, 6 percent had 450 to 474, 5
percent had 475 to 499, and 3 percent had 500 to 530 (Figure 2).

Animal Guilds Based on Life Requirements

Food Requirements

1. General Food Habits. Guilds were established on the basis of general
food habits (i.e., herbivore, omnivore, carnivore) by life stage of the
animal, including larvae, juvenile, and adult. The larval-herbivore guild
contains 131 species, or 16 percent of the 844 animals in the data base;
juvenile-herbivore guild contains 36 species, or 4 percent, and the adult-
herbivore guild contains 120 species, or 14 percent of the 844 animals in the
data base.

2. Larval Food Habits. Guilds were developed using the general food
habits of the larval life stage. Twenty-six categories of food were
identified for larvae. Three of these were selected to demonstrate how the
guilds are developed, and we found that 60 species of larvae fed on organic
detritus; 36 species on aquatic insects, and 38 species on diatoms (Table 7).

3. Juvenile Food Habits. The procedure used in developing larval food habits was applied to juvenile food habits. Again we selected three juvenile food items to demonstrate the process: 68 species of juveniles fed on adult amphibians, 231 on aquatic crustaceans, and 124 on segmented aquatic worms (Table 7).

4. Adult Food Habits. We selected adult food items and followed the same procedure used to develop guilds for larvae and juveniles. We found that 103 species of adults fed on clams, 148 on fish fry, 148 on aquatic snails, and 179 on zooplankton (Table 7).

Niche Requirements

We selected adult resting, feeding, and breeding activities and habitat parameters which may be of interest to the Corps of Engineers.

We also looked at the egg niche requirements and selected four habitat parameters and their subclasses to demonstrate this level of guilding:

pH - 4 subclasses
Oxygen - 4 subclasses
Depth - 3 subclasses
Temperature - 2 subclasses

The results are given in Table 8. The cost of computer time to make the sets in Table 8 was $4.26.

Animal Guilds Based on Non-Biological Characteristics

Status

There are 10 status categories in the data base. We guilded the 844 animals on the basis of this status and group (Table 9). For example, 79 percent of the animals were classified as commercial, 15 percent as consumptive recreation, and 1 percent as endangered by the Federal Government.

Origin

There were six categories of origin for the 844 animals, including exotic, native, feral, stocked, transplanted, and re-introduced. An individual species may appear in several categories. For example, the wild turkey is native, transplanted, and re-introduced in Pennsylvania. We found 95 percent of the animals were native to the state, 5 percent were transplanted, and 2 percent were exotic and stocked. Two species were feral, and four were re-introduced (Table 10).

Management Practices

Management practices are listed as either beneficial or adverse to each species. We guilded the animals according to three beneficial management practices which may be of interest to the Corps of Engineers, including: creation of impoundments, increasing water depth, and stream bank protection. We also guilded the animals on the basis of four adverse

management practices, including channelization, creation of impoundments, impoundment of waterways, and siltation. We guilded the animals on the basis of group as well as management practices (Table 11) and found that 13 percent of the 844 animals would benefit from protection of stream banks and 16 percent would be adversely affected by channelization. Computing costs to make the analysis in Table 11 were $2.50.

Animal Guilds Based on the National Wetland Classification

NWI Systems

We selected three NWI systems* to demonstrate how to guild animals into the major classes of this inventory. We found that 33 percent, 23 percent, and 58 percent of the 844 animals were guilded into the locustrine, palustrine, and riverine systems, respectively (Table 13).

NWI-AHC E 2 AB 2N3

We guilded animals on the basis of the aquatic habitat classes of estuarine, intertidal, aquatic bed, submergent vascular, regular tides, and brackish water. We found 11 species in this guild (Table 13). We guilded these 11 animals according to 15 egg niche requirements, and have reported results by common name.

NWI-AHC R2 SBI HO

We guilded animals on the basis of the AHC, which is riverine, lower perennial, stream bed, cobble/gravel, permanent water, and fresh water. We found 29 species in this guild, including 24 fish, one aquatic insect, two molluscs, one other aquatic invertebrate, and one reptile. To demonstrate different possible guilds, we listed these 29 animals on the basis of group, common name, status, and their occurrence by county (Table 14).

To gain additional information which may be useful in developing guilds, we listed the egg niche requirements by common name. An example of this type of printout for six of the fishes follows:

```
<COMMON-NAME>  BASS, ROCK
<NICHE-E-T>
   WATER TEMPERATURE:MESOTHERMAL,DISSOLVED OXYGEN:MESOXYPHILOUS,
   PH:INDIFFERENT,SUBSTRATE:EPIBENTHIC,VELOCITY:<0.5 FPS,
   SALINITY:OLIGOHALOBOUS,WATER DEPTH PREFERENCE:1-5 FT

<COMMON-NAME>  BASS, SMALLMOUTH
<NICHE-E-T>
   WATER TEMPERATURE:MESOTHERMAL,DISSOLVED OXYGEN:MESOXYPHILOUS,
   PH:NEUTRAL,SUBSTRATE:EPIBENTHIC,VELOCITY:<0.5 FPS,
```

*L.M. Cowardin, Virginia Carter, F.C. Golet, and E.T. LaRue. 1979. Classification of Wetlands and Deep water habitats of the U.S. FWS/OBS-79/31. 103 p.

SALINITY:OLIGOHALOBOUS,WATER DEPTH PREFERENCE:1-5 FT

<COMMON-NAME> CARPSUCKER, HIGHFIN
<NICHE-E-T>
   UNKNOWN

<COMMON-NAME> CATFISH, FLATHEAD
<NICHE-E-T>
   WATER TEMPERATURE:MESOTHERMAL,DISSOLVED OXYGEN:MESOXYPHILOUS,
   PH:ALKALIPHILOUS,SUBSTRATE:EPIBENTHIC,VELOCITY:<0.5 FPS,
   WATER DEPTH PREFERENCE:1-5 FT

<COMMON-NAME> DARTER, BANDED
<NICHE-E-T>
   UNKNOWN

<COMMON-NAME> DARTER, BLACKSIDE
<NICHE-E-T>
   WATER TEMPERATURE:MESOTHERMAL,DISSOLVED OXYGEN:MESOXYPHILOUS,
   PH:NEUTRAL,SUBSTRATE:EPIBENTHIC,VELOCITY:.5-1.0 FPS,
   SALINITY:OLIGOHALOBOUS,WATER DEPTH PREFERENCE:1-5 FT

Applying the Concepts of Animal Guilding in the Review
of a 404 Permit Application

   Project Description:* Elimination of about 1000 acres of freshwater
wetlands bordering Moshannon Creek, Clearfield and Centre Counties,
Pennsylvania, to control flooding and mosquito populations and channelization
of portions of Moshannon Creek.

   Project Area: Moshannon Creek originates near the line dividing Blair
and Centre counties, PA, and flows about 30 miles to its confluence with the
West Branch of the Susquehanna River just south of Karthaus. The project area
includes those wetland habitats bordering Moshannon Creek from South
Philipsburg to Munson, and wetlands along Laurel Run.

   Moshannon Creek between South Philipsburg and Munson is characterized by
a low gradient and meandering channel. A 7800-foot stream section downstream
from Philipsburg was channelized in 1974. In addition, Moshannon Creek is
severely polluted by acid mine drainage from inactive or abandoned deep mines
in the watershed. Because of the stream's low pH, few fish are present in
Moshannon Creek. This, plus the excellent mosquito breeding habitat provided

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*Much of the site-specific habitat information used in this analysis was taken
 from a report prepared by Ms. Cynthia Rice and Mr. Michael Chezik, U.S. Fish
 and Wildlife Service, State College Field Office, State College, PA. Their
 findings are summarized in the report, "Summary of Biological Investigations
 in Wetlands Bordering Moshannon Creek from South Philipsburg to Munson,
 Clearfield and Centre Counties, Pennsylvania: 1977-1981 (U.S. Department of
 the Interior, 1981).

by the bordering wetlands, contributes to spring and summer mosquito outbreaks. Insecticides are applied throughout this period to reduce mosquito populations.

The wetland and forest habitats bordering Moshannon Creek and Laurel Run were used to define and structure data base requests that identify a potential list of species on the project area and impacts on animals if the stream is channelized and the wetland habitat altered. We analyzed the impacts of the proposed activities using a question/response approach. The results follow:

Q1. What species occur in the Moshannon Watershed (Office of Water Data Coordination Hydrologic Unit 02050201) and Clearfield/Centre Counties guild?

R1. There are 442 species known to occur in Clearfield or Centre Counties and the Moshannon hydrologic unit guild. These are:

Group	No. of Species
Amphibians	21
Birds	231
Fish	50
Aquatic Insects	8
Terrestrial Insects	48
Mammals	50
Molluscs	6
Other Terrestrial Invertebrates	4
Reptiles	24
Total	442

Q2. Of the 442 species potentially occurring in the Moshannon <u>Project Guild</u> (a specific portion of the entire Moshannon Watershed), what species are associated with the wetland and forest habitats guild?

R2. 350 of the 442 species in the Moshannon Watershed (large area) are associated with the habitats identified in the Project Area.

Q3. Of the 350 species potentially occurring in the Moshannon Creek Project Area (that is, typically associated with the types of habitats occurring in the Project Area and known to occur in the watershed), do any of these species have Federal or State endangered or threatened status?

R3. None.

Q4. Are any of the 350 species potentially occurring in the Moshannon Creek Project Area considered extremely sensitive to environmental/habitat changes?

R4. Yes; there are seven species in this guild which are listed as being sensitive to environmental/habitat changes, including:

Group	Species
Amphibian	Peeper, Northern Spring
Bird	Eagle, Golden
Bird	Goshawk, Northern
Bird	Loon, Red-throated
Bird	Osprey
Fish	Bass, Large-mouth
Fish	Trout, Brook

Q5. Which of the 350 species potentially occurring in the Moshannon Creek
     Project Area require alkaline pH values to complete their life cycle;
     that is, which species would definitely not occur in Moshannon Creek if
     waters were acidic?

R5. Seven species would not occur in Moshannon Creek if waters were acidic.

Group	Common Name
Fish	Bowfin
Fish	Chub, Creek
Fish	Crappie, Black
Fish	Dace, Pearl
Fish	Trout, Brown
Fish	Trout, Rainbow
Fish	Stoneroller

Q6. What species would be adversely affected by channelizing Moshannon Creek,
     increased siltation from runoff, and applications of insecticides?

R6. There are 37 species that would be adversely affected in Moshannon Creek.

Q7. In addition to the 37 species that would be affected by the conditions
     specified in questions 5 and 6, which species would be adversely affected
     by the elimination of streamside vegetation?

R7. An additional 66 species would be adversely affected by the removal or
     elimination of streamside vegetation. Fifty-eight of the 66 species are
     birds, four are mammals, and four are reptiles.

     The total time and cost for querying the data base and developing these
guilds include:

   a. Biologist: identification of project area characteristics, struc-
       turing data base queries (@ $10/hour x 1 hour) = $10

   b. Computer Costs: (126 connect minutes) = $37.90

   c. Computer Operator (@ $10/hour x 2.1 hours) = $21.00

   d. Telephone (long distance commercial rate @ $18/hour x 2.1 hours)
       = $37.80.

                        Total Cost = $106.70

Substantial reductions in cost were possible if detailed information for all vertebrate and invertebrate species was not included in the guild. For example, determining whether endangered or threatened species occur on a particular area could be done in one or two queries at a computer cost of less than two dollars.

In summary, we found no endangered or threatened species in the Moshannon Creek Project Area. Some of the seven "sensitive" species are likely to be adversely affected by wetland alterations; however, all of these species are migratory or species commonly occurring in other areas within the state.

Field investigations (about 25 person-days over 5 years) identified 81 species of animals in the project area. The Pennsylvania Fish and Wildlife Data Base was used to identify, in a couple of hours, a guild of 350 species likely to occur on the project area. Proposed channelization and subsequent reductions in streamside vegetation, along with increased siltation, would eliminate potential habitat for some groups of animals.

Species on the Project Area No. Alterations	Species on the Project Area Following Group	Habitat Alterations
9	Amphibians	6
188	Birds	116
50	Fish 33	
45	Terrestrial Insects	45
4	Other Terr. Invertebrates	4
37	Mammals	31
17	Reptiles	12
350	247	

Conclusions/Recommendations

Conclusions

We have demonstrated one approach to guilding animals using a computerized fish and wildlife information system. The effectiveness of this approach will depend primarily on the user's information needs and how each user defines guilding. Guilding or grouping animals using computerized procedures can be done quickly to address a wide range of situations and proposed alterations of habitat. The effectiveness of these data is a function of the quality and quantity of information in the system. Based on five years experience and working with a number of State and Federal agencies in developing and implementing computerized animal data bases, we offer the following recommendations to the Corps of Engineers concerning the use of the concept of guilding animals for impact assessment and resource management, irrespective of which system or approach is selected.

Recommendations

1. Available data on animal species should be compiled in a standard format for computer listing and management. This maximizes use of available

information, provides a means to identify gaps in knowledge, and provides a repository for new information.

2.   Data compilation should be a cooperative State, Federal, and private effort. No single agency has the expertise, facilities, capability, or funds to complete the task alone. The synergistic effects outweigh the cost of coordination.

3.   Long-term management responsibility of an animal data base should reside with the State fish and wildlife agency. This agency has legal responsibility for the management of the resident animals--about 95 percent of the 844 animals in Pennsylvania. This agency also has more stability than Federal programs and will most likely ensure availability of quality information to a wide variety of users.

Region	Subregion	Accounting Unit	Cataloging Units
		01	01,03,04,05,06
02	04	02	01,02,03,05
Mid			
Atlantic		01	01,03,04,05,06,07
	05	02	01,02,03,04,05,06
		03	01,02,03,04,05,06
	06	00	02,03
	07	00	02,03,04,09
	11	00	03
04	12	01	01
Great Lakes	13	00	02
			01,02,03,04,05
	01	00	06,07,08,09
05			
Ohio	02	00	03,04,05,06
	03	01	01,02,03,04,05,06

Figure 1

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SOLVING ENVIRONMENTAL PROBLEMS USING THE PPLV
APPROACH AND GUILD THEORY

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Approximately 6 weeks ago, a new version of the National Contingency (i.e., "Superfund") Plan was released for comment. This most recent revision marks a drastic departure from previous positions maintained by the Environmental Protection Agency (EPA). Those positions were characterized by rigid enforcement of standards for environmental control. By contrast, the new position espoused by EPA has been criticized for being too vague. Between these two extremes, there must be a more reasonable central position. Clearly, the EPA recognized some of its former faults, in particular the tendency to rely on predetermined rules in dealing with unforeseen new situations; it sought to correct these by applying a "flexible standard for determining the appropriate extent of remedy." It chose, in truth, to adopt a fairly inflexible means—the MITRE Hazard Ranking System—for selecting sites for remedial action (i.e., defining "how dirty is dirty?"). It opted for confusion (no standards whatsoever) in determining the extent ("how clean is clean?") of remedial action. Both choices give little comfort to the dedicated ecologist. In the selection of sites, the criteria are based entirely on the impact on human health; by implication, the same will probably be true for methods that may be selected for determining how far to go with remedies.

It might be appropriate, while matters are still being settled, for the ecologist to raise a voice in protest, but it would be better still to propose constructive solutions. Fortunately, there is a decision-making approach, already applied to human health effects, that could be adapted to impacts on the ecosystem. We refer to this as the Preliminary Pollutant Limit Value (PPLV) process. The process is site-specific and involves examination of the potential for each chemical of concern to proceed from its points of origin in the soil or water, through defined pathways, to man or any other target species. Each pathway is treated as if it consisted of a series of compartments at equilibrium, except that the exposure of the target species to the last of these compartments is handled as a rate process. Where possible and desirable, one utilizes available toxicological information to define an acceptable daily dose, D_t, for the organism's exposure to each compound and calculates levels of the compound in the soil or water such that D_t is not likely to be exceeded under a given set of conditions.

There are some differences between application of the PPLV process to man and to species in general. In the former case, focus is on the individual's well-being and life; in the latter, it is on the viability of the species and its balance with the rest of the system. Pathway analysis, leading to estimated exposure levels, is the same in both cases. For animal or plant species threatened with disappearance from an area, we can improve on the concept by using non-endangered guild-mates as surrogates for the endangered species. These occupants of similar ecological niches can be collected in sufficient number and sacrificed for tissue samples without a significant

population impact. In this way, application of the guild theory contributes to the preservation of rare or endangered forms of life. One caution to be voiced is that the acceptable daily dose (i.e., level of exposure) for one species is not necessarily the same as that for a guild-mate. Application of guild theory cannot assure comparable physiological responses to foreign compounds, even though a degree of similarity may exist in dietary patterns and diurnal behavior. Thus, we must favor a conservative estimate in setting allowable exposure levels. Some toxicological testing may be feasible with an endangered species, but it cannot be nearly as extensive as one might like. It is also possible to use nonguild-mate surrogates; for example, the mink as a surrogate for the badger.

We believe the PPLV process to be more adaptable than the Hazard Ranking System for determining which sites must be modified to protect endangered species. In Louisiana, no remedial action is planned now under "Superfund," and plans are actually under way to establish more waste disposal facilities there. Care is not being exercised to protect the environment and its fauna. It will be necessary to call attention to this omission. We should be able to apply the PPLV methodology, in conjunction with the guild concept, to protect the most vulnerable members of our environment, as well as ourselves.

THE CORPS: WHERE DO WE GO FROM HERE?

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Not everyone agrees with the current status and application of the guild concepts, so it is difficult to project a future direction. On the other hand, this uncertainty provides unlimited opportunity for the future. I'd like to describe why and how we do research in the Corps, and then use that as a basis to look at "the big picture" to get an idea of what we might be doing and how we might be proceeding.

At USA-CERL, we look at research in two ways: inventive and innovative. By inventive research, we are referring to basic research whose objective is to develop state-of-the-art or to improve state-of-the-art technology. This type of research is done primarily through academic efforts. When we speak of innovative research, we are referring to refining technology to solve some problem the Army has, and this is the main thrust of the work we do at USA-CERL. We apply available technology to dealing with an existing problem. Occasionally, we may find that there are technology gaps—that we cannot solve our problems with available technology. In those cases, we will undertake some basic research. But primarily, we are appliers of technology, and this is our primary interest.

Very briefly, I would like to talk a little bit about why we do research in the Corps. We realize at USA-CERL that it is not the Army's mission to protect the environment. That's just the way it is. However, they do have compliance requirements; the mission statement of the Environmental Division is to provide support necessary to preserve environmental quality while at the same time supporting the Army's training and readiness missions, and so forth. So we work in this type of environment, that we do research when this capability to support the Army does not exist. Cost, of course, is another reason for doing work. If you can do your job, money is no object; you have unlimited funds, so you don't need any kind of research. But if resources are short and you want to do a job and you want to do it for the least cost, then research may be necessary to bring down these costs. Cost is always a basis for doing research. We also go a little bit beyond that. Capability and cost is what impresses the people who fund our research, but we also like to take advantage of technology opportunities. Even if the capability seems adequate and there are funds to do the job, it may still be possible to do things better at less cost. And also, to take advantage of some of these opportunities, individual researchers do like to make a contribution to science whenever possible.

Generally, I think the best way to approach research is to identify a problem and then try to develop some solution to it. An example of this is people coming up to a remote sensing researcher and saying, "What can remote sensing do?" "What kind of information can you give me on remote sensing?" That's not the way to approach the problem. The way to do it is to say, "I have certain information requirements—can you design me a system that will meet those requirements?"

Well, I'm not going to follow that theoretical pathway. Instead, let's just assume that guilds are the solution and take a look at what the utility of some of these things might be. And, of course, we're talking about some sort of guilds, plus whatever classification or terms you want to use. I think these categories of utility are pretty easily understood. We like to develop a basic understanding of the processes. We like to have the predictive capabilities. We're interested in assessment techniques, evaluation techniques, monitoring, planning, and management. Now when we first started being interested, we were looking primarily at predictive capability and assessment techniques. Generally, we concluded that there was just no effective capability of looking at biological systems and doing assessments the way we wanted to do them and being able to make predictions, largely because of the complexity of the environment. This is when Bill Severinghaus decided that this might be a way to solve the problem of complexity. At USA-CERL, we are committed to guilds or some type of guilds approach, and we think that this is going to help solve problems on military installations and that it will be useful in planning and management. We are going to pursue this line of research.

Now we come to the problems of where we go from here. This looks pretty complex, but I'll try to explain some of the ideas I had in putting this together. I think there is a basis for deciding what type of strategy we want to use in pursuing development of guilds. The first thing we need to do is to define our objectives. Then, based on these objectives, we can look at strengthening the terminology. In listening to the discussion over the last couple of days, it seemed to me that at one time someone would say, "let's keep flexibility, we don't want any rules." Then, a little bit later, someone would say, "you're not following the rules for how guilds are supposed to be used." My point is that I don't see how people can follow the rules when there are no rules. Eventually, it seems that the consensus was that if you define what you're going to use these techniques for (your objectives), then you can define some sort of terminology. That's something that certainly needs to be done.

There were also discussions about the overemphasis on birds instead of the other areas. As you begin to go through some sort of strategy for working, you can branch out into a lot of other areas--mammals, birds, and vegetation. Fish seem to be the ones that people have worked in, and there are probably a lot of other ones too. For any given pathway, I'm suggesting that here are some steps in the research process that must be considered, and we've had some discussions during this conference on how this could be done. Define resource gradients. The Army and probably the Corps in general have to manage using a lot of factors. I think the two-dimensional approach to defining resource gradients may not be completely satisfactory. For example, at military installations, there are a lot of effects on animals and vegetation, other than just food sources and habitat. We have things like noise, vehicles moving through, chemicals being used, smokes, and so forth, so I think there must be a lot of attention given to what resource gradients will be used and how they will be defined.

I think a lot of the discussion last night centered on the next step-- classification techniques. Can you use an analytic technique, can you use cluster analysis, or can you use some other method to come up with these classification schemes? That's a topic that must be addressed. Then, of

course, we must come up with some sort of classification scheme. My feeling
is that for these first steps to be effective, and for these to be applied in
the field, there must be some type of application guidelines. I think that
the information which comes out of these steps would fit into the development
of some sort of application guidelines for developing these classification
schemes. Of course, once you come down a pathway (such as mammals or birds or
all of them), you begin to become interested in the interrelationships among
these different technical areas. We can also look at developing analysis
techniques; that is, how do we use these classifications to make some
difference in our planning and management activities? Then we can develop
predictive techniques for monitoring and assessments, and also develop a basic
understanding of what's going on with some of these processes. There was also
a lot of interest in quantification; i.e., is it good, is it bad, how do we do
it? In my opinion, the main problem with quantification was the fear that the
decision-maker would use numbers instead of reasonable judgment. Therefore,
I'm suggesting that sometime we may want to pay some attention to something
which I'll just call a translator. This is nothing more than the interface
between the environmental planner and the decision-maker. What I'm saying is
that it may not be necessary that the decision-maker receive any quantitative
information. He may receive this information in some other form, but that's
certainly a problem I think that must be looked at. Then, of course, using
these techniques, the payoff is better planning and management.

To summarize, it seems that the opportunities are great for doing a lot
of things with guilds. Perhaps the next step on the applications side is
defining our objectives. What is it we want guilding to do for us or some
other classification? I also think that after we have this as a basis, we
must work out what the rules are going to be. I think it's very important
that there be agreement in terminology and what type of rules are going to be
followed. Then I suggest that people just start applying it and start
building up some experience with using it--just carrying on what's been done
so far.

CLOSING REMARKS: CONFERENCE ON THE APPLICATIONS OF THE GUILD CONCEPT TO ENVIRONMENTAL MANAGEMENT

William D. Severinghaus, U.S. Army Construction Engineering
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The University of Illinois and the U.S. Army Corps of Engineers sponsored a conference to discuss existing use within basic and applied ecology for classifying organisms into functional units (guilds). The meeting was held in Chicago at the Sheraton-O'Hare Hotel, April 20-22, 1982, and was attended by a cross-section of scientists representing State and Federal government agencies, academic institutions, and private enterprise.

The first part of the conference was devoted to a discussion of (1) the need for functional classification in ecology, as compared to taxonomic or phylogenetic classification; (2) the development and meaning of the guild concept; and (3) the manner in which guilding is interpreted by the academic community. Major contributors to this discussion were Richard B. Root, Cornell University, who originally defined the guild concept (1969); Peter W. Price, Northern Arizona University; Timothy C. Moermond, University of Wisconsin; and Julie S. Denslow, University of Wisconsin. After the formal presentations, which crossed the general fields of entomology, botany, herpetology, ornithology, ecology, and evolution, the discussion centered on discrepancies between the definition of a guild and the manner in which the concept is being interpreted.

Although there was no general agreement on the definition or appropriate use of the term "guild," it was agreed that individual scientists undertaking functional classification and using the term "guild" should clearly define their use, including the purpose for their classification.

The second portion of the conference delved into the use of guild classifications within the "classical" management disciplines of forestry and wildlife management. Principal contributors were Henry L. Short, U.S. Fish and Wildlife Service; Jared Verner, Forest Services Laboratory; and Richard M. DeGraaf, Urban Forestry Research Unit. Their applications-oriented presentations concentrated on birds, with discussions of "guild block" matrices, guild indicator versus guild unit approaches, and guild density. Again, the need for precision in definition of usage was emphasized. The usefulness of guilds as a clustering tool for monitoring, the advantages of the "unit" approach, and the ability of guild-based studies to discern change at various temporal and spatial scales were discussed.

The next session dealt with application of the guild concept to contemporary problems of environmental monitoring and management. Major contributors were James R. Karr, University of Illinois; Gary D. Schnell, University of Oklahoma; James D. Felley, McNeese State University; and Steven I. Apfelbaum, Ecological Research Services. The need for biological monitoring in combination with physical and chemical monitoring was stressed; use of the guild concept in the form of community guild signature (percent distribution of guilds) was discussed as a key component of biological monitoring programs. The development of an "index of biotic integrity" and

the importance of species lists were discussed. Soil and plants were discussed as they pertain to the uniqueness of reclamation, nature preserves, and the problems of applying ecological generalizations across a wide variety of site-specific problems.

During the final session, several research programs that use the guild concept were discussed. William D. Severinghaus, U.S. Army Construction Engineering Research Laboratory (USA-CERL); Charles T. Cushwa, Fish and Wildlife Service; Edward W. Novak, USA-CERL; and Robert J. Kainz, U.S. Army Medical and Biological Research and Development Laboratory discussed new twists to studies based on guilds. Formal presentations dealt with use of guild-based classification schemes in environmental analysis, prediction, and mitigation; use of computerized data bases for guild membership delineation; and use of the guild concept in examining hazardous and toxic waste pathways through ecosystems.

In summary, the major points raised were (1) the imprecision of the concept of guild classification within and between academic and applied ecological research communities; (2) the need for functional classification to help define problems and analyze management goals; (3) the potential for the guild concept in applied ecological research; (4) the weak status of statistical procedures for using the guild concept in applications-oriented studies.

Other technical and organizational contributions were made by Peter B. Landres, Utah State; Robert E. Riggins, USA-CERL; and John Belshé U.S. Army Corps of Engineers.

A publication summarizing the conference conclusions is being developed. Those desiring further information prior to availability of the publication should contact William D. Severinghaus, USA-CERL, P.O. Box 4005, Champaign, IL 61820 (217/352-6511).

APPENDIX A:

TECHNIQUE FOR STRUCTURING WILDLIFE GUILDS
TO EVALUATE IMPACTS ON WILDLIFE COMMUNITIES

APPLICATION OF THE GUILD CONCEPT TO ENVIRONMENTAL
IMPACT ANALYSIS OF TERRESTRIAL VEGETATION

AN ECOLOGICAL CLASSIFICATION FOR FRESHWATER
FISH SPECIES OF THE CONTERMINOUS UNITED STATES

Technique for Structuring Wildlife Guilds to Evaluate Impacts on Wildlife Communities

by

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Abstract

This paper describes a technique for ordering wildlife information according to physical strata and vegetative structure so that a variety of statistical analyses can be accomplished. Individual wildlife species are assigned to cells in a species-habitat matrix on the basis of feeding and breeding activities within physical strata in representative types of vegetative cover: the cells within the species-habitat matrix are assigned numeric values. The statistical analyses are thus based on the areas that individual species occupy within the species-habitat matrix. Computer graphics are used to represent the structure of wildlife communities and cluster analysis routines are used to describe the potential wildlife guilds that may exist in different vegetative communities. Different numbers of wildlife guilds will occur in different types of cover within a potential natural vegetation type. Furthermore, the number of wildlife species and presumably also of wildlife guilds present within a type of cover is modified by physical attributes of the vegetation within that cover type. The products of this analytical technique may be suitable for evaluating habitat quality, impact assessments, regional inventories and assessments of wildlife resources, and land-use planning activities.

We describe in this paper a technique for relating wildlife species to the structure of vegetative communities so that one can predict the impacts on wildlife communities that will occur as vegetative communities are changed. The technique has a numeric basis so that a variety of computer simulations and analyses can be accomplished to describe wildlife-habitat relationships.

The concepts in this paper were developed with a data base compiled for the eastern ponderosa pine (*Pinus ponderosa*) forest (Küchler 1964, type 16). Data about wildlife species occurring in southeastern Montana and northeastern Wyoming were determined from the literature, were organized according to a species-habitat matrix, and were subjected to statistical analyses. Results of those statistical analyses include graphic illustrations that indicate the dependencies of individual species on the structure of vegetative cover types, and the development of groups of species, called guilds, which utilize similar food sources and breeding niches within habitats for their support and well-being. The structure of wildlife communities that might exist within three different cover types of the eastern ponderosa pine forest type is presented in detail and lists of guilds (and their membership) within each type of cover are described.

Development of our technique has been strongly influenced by the current state of the art for evaluating habitat quality for wildlife, reviewed in detail by Erickson et al. (1980). We have been especially influenced by (1) models that evaluate habitat quality on the basis of the habitat's ability to satisfy life requisite needs of selected animal species, (2) prediction models of wildlife habitat quality that rely on map-based criteria identified from aerial photography, (3) computerized and noncomputerized data bases for wildlife species, and (4) computer simulation models of ecosystem functions.

Our wildlife guilds are aggregations of species that tend to utilize the resources of a habitat in a similar manner. These guilds are closely tied to the structure of vegetation and have a numeric basis so they can be used in habitat simulation and modeling. Thus, if changes in the structure of vegetation can be predicted from some land use, then the probable impacts on wildlife guilds caused by change can also be predicted. In addition, we distinguish between primary and secondary consumer activities for an individual species, if appropriate, so that an omnivorous species can be shown as competing with one group of species as a primary consumer and with a second group of species when acting as a secondary consumer. Our guilds

are less specialized than those advocated by Root (1967) which are associations of species with very similar foraging strategies and habitat requirements. Our guilds, on the other hand, are more specific and meaningful than are artificial classifications or groupings of species based on size, food habits, and foraging strategies (Severinghaus 1981), and seem to provide a greater analytical and predictive capability than does the life form concept of Thomas (1979).

Our guilding technique allows habitat evaluations and assessments to be meaningfully based on a community principle rather than on selected indicator species. Advantages include those of thoroughness and even-handedness in the treatment of all segments of the wildlife community and an enhanced opportunity for interpreting wildlife data with data from other land uses in planning efforts. The potential applications cited in the Discussion section are presumed and not proven. Ongoing research will evaluate the usefulness of the present concepts in natural resource management. Although the analyses, examples, and discussions presented here are directed toward terrestrial communities, the statistical assessments should be equally relevant to aquatic systems.

Six assumptions were made to develop the information presented in this paper:

1. That complex biological requirements of animals can be structured into a two-dimensional matrix, and that energy sources and breeding requirements are so basic that they can meaningfully represent the axes of that matrix.

2. That ordering vegetative cover types into a series of vertical strata is a natural organizational framework within the two-dimensional matrix.

3. That major food sources "of similar importance" can be identified and that these food sources can be organized in a rational manner within the strata of the matrix.

4. That major breeding niches "of similar importance" can be identified and that these breeding niches can be organized in a rational manner within the strata of the matrix.

5. That the biological information about individual species is sufficiently detailed in the literature so that feeding and breeding requirements can be compiled for each wildlife species occurring within a cover type.

6. That the abstract numerical designations given to the food source and breeding niche listings can be subjected to numerical and statistical analyses.

Methods

The development of a technique for translating a variety of descriptive data about wildlife species into a numerical framework was basic to our technology. The biology of any wildlife species is exceedingly complex and many of the biological requirements for any species are poorly known. Simplification of a complex, varied, and poorly known biological universe was obviously required.

We selected energy sources and physical breeding requirements as the basis for organizing wildlife information in our guilding analyses. These two criteria are obviously fundamental to the existence of species, are driving forces affecting the behavior of species, and are sufficiently gross parameters so that adequate information might be available for most wildlife species.

We then developed a simple two-dimensional species-habitat matrix with energy sources along the y-axis and physical features of the habitat required for breeding along the x-axis. The y-axis was subdivided so that the lower half of the y-axis could provide loci for data about primary consumers, and the upper half of the y-axis could provide loci for data about secondary consumers. Both axes of the matrix are partitioned by physical strata, because numerous authors have emphasized the importance of strata in describing the form and function of ecological communities. The food sources for animals comprising the y-axis of the matrix are organized as indicated in Fig. 1. The 191 food sources representing the rows of the matrix are identified in Appendix I. The physical features required for breeding (the x-axis of the matrix) are organized as indicated in Fig. 2. The 238 columns representing breeding requirements are identified in Appendix II. The numbers assigned to rows and columns of the matrix are those listed in Appendices I and II.

Feeding and breeding criteria for a species are located in the species-habitat matrix by listing the numeric x and y coordinate values which identify the cell or cells within the general matrix that best describe the habitat requirements of that species. For example, the Steller's jay (see Appendix III for scientific names of vertebrates) occurs in the mature-tree stage of ponderosa pine in the eastern ponderosa pine type of woodland (Küchler 1964, type 16). This jay consumes a variety of insects and herbaceous and pine seeds on the ground and a variety of insects and pine seeds in the pine canopy. Its nest is a bowl of coarse twigs, usually placed in the crotch of a horizontal tree branch within the pine canopy. The x and y coordinates (Appendices I and II) that best describe the requirements of the Steller's jay inhabiting mature ponderosa pine woodlands are listed in Table 1. The data in Table 1 fill the cells in the matrix indicated in Fig. 3.

We have used the concept of potential natural vegetation as a convenient bound for our data sets. The potential vegetation types of Küchler (1964) are areas that presumably produce vegetation of a common taxa and structure if left undisturbed for a sufficiently long period. Presumably the same wildlife community also will eventually develop throughout this type of climax vegetation. The structure of this wildlife community (guilds) could thus potentially be similar throughout this climax vegetation type. These potential guilds can be considered a standard of comparison for the wildlife communities found in current cover types within the potential natural vegetation type. The potential vegetation type is also a useful bound because its area, and the numbers of cover types (current vegetative

Feeds elsewhere
(3.0)

Aerial feeders
(2.3)

		Tree canopy	(2.25)
		Tree bole	(2.24)
		Shrub	(2.23)
		Terrestrial surface	(2.22)
	Terrestrial feeders (2.2)	Terrestrial subsurface	(2.21)
		Surface of water column	(2.13)
		Water column	(2.12)
Secondary consumers (2.0)	Aquatic feeders (2.1)	Bottom of water column	(2.11)

		Tree canopy	(1.25)
		Tree bole	(1.24)
		Shrub	(1.23)
		Terrestrial surface	(1.22)
	Terrestrial feeders (1.2)	Terrestrial subsurface	(1.21)
		Surface of water column	(1.13)
		Water column	(1.12)
Primary consumers (1.0)	Aquatic feeders (1.1)	Bottom of water column	(1.11)

Fig. 1. Organization of food sources by strata along the y-axis of the species-habitat matrix.

types) and wildlife species present in those cover types are not unmanageably large.

We developed data sets describing the x and y coordinates of wildlife species in the climax ponderosa pine type in southeastern Montana and northeastern Wyoming, and also for six additional current vegetation types found in that potential natural vegetation type. Those additional vegetation types are sagebrush steppe (*Artemisia* spp.), upland grassland, riparian grassland, riparian shrubland, riparian woodland, and aspen (*Populus* sp.). Only the data for the upland grassland, sagebrush steppe, and the ponderosa pine type are extensively discussed in the present paper. Data for the other types are included in summary tables. A data base containing the appropriate numeric x and y coordinates was developed from the literature for each of the 275 nonfish vertebrate species resident and breeding in this potential vegetation type (Appendix III). The numeric data in the data base were structured into a computerized data file, which was then manipulated to produce the various displays and summaries given in the Results section.

Each pair of x and y coordinates developed for a species in a vegetation cover type represents either a primary consumer or a secondary consumer role. The average x and y values (and their standard deviations) were calculated for the data describing the primary or secondary consumer role for each species in a data set. These means and standard deviations summarize the feeding and breeding data for each species in that data set. Standard deviations of 0 were listed if only a single x and y coordinate existed for the primary or secondary consumer role of a species. The means and standard deviations for the data about Steller's jay (Table 1) are also listed in Fig. 3.

Simple and portable computer programs (FORTRAN) were written for checking the basic data, computing the summary statistics, and printing various summaries. The

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Aquatic system - tidal
(1.0)

High dissolved solids content
(1.1) (marine system)
- Bottom (1.11)
- Column (1.12)
- Surface (1.13)

Moderate dissolved solids content
(1.2) (estuarine system)
- Bottom (1.21)
- Column (1.22)
- Surface (1.23)

Aquatic system - nontidal
(2.0)

Temporary water
(2.1)

Permanent water
(2.2)
(riverine, palustrine,
and lacustrine systems)

Cold water (2.21)
- Bottom (2.211)
- Column (2.212)
- Surface (2.213)

Cool water (2.22)
- Bottom (2.221)
- Column (2.222)
- Surface (2.223)

Warm water (2.23)
- Bottom (2.231)
- Column (2.232)
- Surface (2.233)

Terrestrial system
(3.0)
- (3.1) Terrestrial subsurface
- (3.2) Terrestrial surface
- (3.3) Shrub strata
- (3.4) Tree bole
- (3.5) Tree canopy

Breeds elsewhere
(4.0)

Fig. 2. Organization of breeding habitats by strata along the x-axis of the species-habitat matrix.

data in the species-habitat matrices are displayed in the Results section in a series of plots that graphically depict the increasing complexity of wildlife communities as vertical terrestrial strata are added. These graphics appear as ellipses developed from the summary $\bar{x}$, $\bar{y}$, SD_x, and SD_y data for all species within a habitat. The ellipses are centered on $\bar{x}$, $\bar{y}$ with semi-axis lengths of one standard deviation (SD_x and SD_y). Two ellipse plots for the data in Table 1 are listed in Fig. 3 to describe the position in the species-habitat matrix occupied by Steller's jay. The data describe the jay as both a primary and secondary consumer.

The ellipse plots were created by using CALCOMP graphics software. Only a small driver program (in FORTRAN) was needed to read the summary data files and call the plotting routines. CALCOMP plotting software is available for many computer systems.

The ellipse plot is only one of the possible ways to associate the structure of wildlife communities with that of plant communities. Graphics that indicate the number of species occupying individual cells in the matrix (bar graphs or numerical values) or present this information as a response surface may also be useful in visually transmit-

ting an impression of the structure of a wildlife community.

The summary data ($\bar{x}$, $\bar{y}$, SD_x, and SD_y for primary and secondary consumer roles) were further analyzed with cluster analysis routines to provide a statistical grouping of wildlife species that use similar resources within ecological communities (guilds).

Cluster analysis provides an efficient grouping of species within habitat types and portrays this information as a phenogram (i.e., dendrogram). The formation of phenograms from x,y data is described in the Results section. Everitt (1974) and Sneath and Sokol (1973) provided an introduction to cluster analysis and computer programs for cluster analysis which are widely available. The software package NT/SYS used for these cluster analyses is a system of multivariate statistical programs that was developed by Rohlf et al. (1979), although almost any set of routines for cluster analysis could be used. We used the unweighted pair-group method with arithmetic averages (UPGMA) in conjunction with the euclidean distance between data vectors ($\bar{x}$, $\bar{y}$, SD_x, and SD_y) as the dissimilarity measure, as recommended by Rohlf et al. (1979). This is perhaps the most common cluster method (see Rohlf et al.

Table 1. *The x-y coordinates for feeding and breeding of Steller's jays in the mature-tree stage of ponderosa pine in the eastern ponderosa forest type.*

Consumer	Feeding coordinate y [a]	Breeding coordinate x [b]
Primary consumer	54	229
	54	233
	56	229
	56	233
	57	229
	57	233
	58	229
	58	233
	60	229
	60	233
	85	229
	85	233
Secondary consumer	159	229
	159	233
	181	229
	181	233

[a]Appendix I.

[b]Appendix II.

1979:72; Everitt 1974:17, group average method; Sneath and Sokol 1973:124, 230–234).

The cluster analysis program used also computes a "cophenetic" correlation coefficient, R, which is a measure of how faithfully the phenogram (i.e., results of the cluster analysis) represents the information in the original data. It is a way of objectively comparing different clustering results. Sneath and Sokol (1973:278–280) provided information about the cophenetic correlation coefficient.

The y-axis of the species-habitat matrix separates primary and secondary consumers so that guilds from phenograms represent only a single role. About 25% of the guilds (12 of 52) produced when the y-axis was not split into primary and secondary consumer roles contained both primary and secondary consumers (Table 2). This was counter to our intended purpose which was to group into guilds only those species that used the resources of a habitat in approximately the same manner. The occupied cells within the species-habitat matrix, when the y-axis was split, represented sufficiently unique patterns so that wildlife species were aggregated into ecologically meaningful groups. The quality of these guilds (aggregation of species) was not improved (judging from the cophenetic correlation, R) by weighting or distorting average Euclidean distances between groups of species within the matrix by arbitrarily increasing the distance along the x-axis of the matrix by a factor of 2. Calculations with raw or unstandardized data (simple means and standard deviations determined directly from data like that in Table 1) produced guilds whose members shared similar strata blocks with better fidelity than did guilds developed from
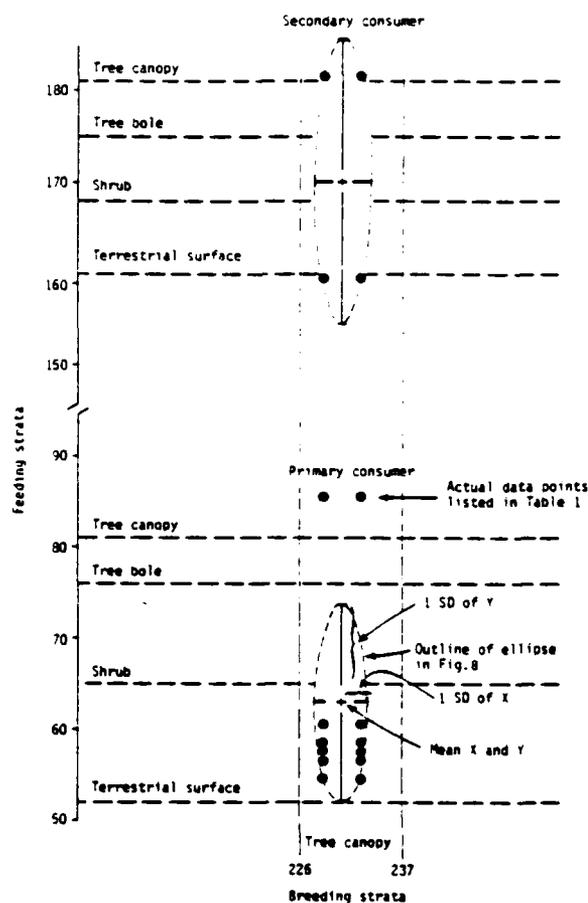

Fig. 3. The x and y coordinate values for Steller's jay (listed in Table 1) and the $\bar{x}$, $\bar{y}$, SD$_x$, SD$_y$ values for these data are plotted on the species-habitat matrix. The elliptical plots indicating the relative areas occupied by the data within the matrix are also plotted in this figure.

data that were standardized by a mathematical transformation that produced unit variances for the x and y coordinates for each species. The phenograms and guilds represented in the Results section were therefore developed with unstandardized and unweighted x and y values in the species-habitat matrix.

The x and y coordinate values for wildlife species can be compiled for both the climax vegetation in a potential vegetation type and for the different actual vegetative cover types and their seral stages within a potential vegetative type. The data set that is produced when the x and y coordinate values are compiled for the wildlife species occupying the climax vegetation can be analyzed to describe a potential wildlife community that can then be used as a standard of comparison in habitat evaluation studies. The data sets that are produced when the x and y coordinate values are compiled for actual vegetation types

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Table 2. *The effect on guild fidelity of using (1) clumped and divided consumer classes within the species-habitat matrix, (2) scalar multipliers, and (3) standardized and unstandardized data in cluster analysis. Data are for a riparian woodland habitat.*

| | | | No. of guilds containing | | | | |
Treatment	Distance for guild determination	No. of guilds	Both primary and secondary consumers	Inconsistent breeding strata[a]	Inconsistent feeding strata[b]	Both inconsistent feeding and breeding strata	Percent of guilds containing inconsistencies
Clumped consumers (152 species standardized)	0.31	52	12	7	2	2	32.7[c]
Divided consumers (92 primary and 139 secondary)							
Standardized							
Unweighed X	0.36	73	0	2	17	3	30.1
Weighed X	0.52	57	0	2	22	1	43.9
Unstandardized							
Unweighed X	3.6	73	0	6	5	1	16.4
Weighed X	5.2	65	0	3	10	1	21.5

[a]At least one guild member uses breeding strata different from its guild partners.
[b]At least one guild member uses feeding strata different from its guild partners.
[c]Seventeen total guilds with inconsistencies.

within a potential natural vegetation type can be used in impact analysis studies to predict the structure of the wildlife community at a future time when one of those actual vegetation types is hypothesized as the vegetation present at that future time.

The x and y coordinate values for wildlife species occupying a vegetation type could become entries in a computerized data base. A person would determine the structure (guilds) of the wildlife community in a particular vegetation type by (1) obtaining a computer listing of species occurring in that vegetation type, (2) obtaining the x and y coordinates for each species, and (3) subjecting that information to the several statistical analyses described earlier in this section.

Results

Wildlife habitat can be considered in terms of guild blocks. A guild block is formed from a two-dimensional matrix where the y-axis consists of strata where food sources can be found and the x-axis consists of strata where breeding habitats occur. A single guild block is formed from the intersection of a foraging habitat stratum and a breeding habitat stratum. Guild blocks can be thought of as a first approximation of the ways in which wildlife species can utilize a type of habitat. For example, there are nine general ways in which wildlife can utilize the upland grassland habitat. Species can breed (B) in the subsurface

stratum and feed (F) in the subsurface stratum; B in the subsurface stratum and F on the surface; B in the subsurface and F in the air; B on the surface and F in the subsurface; B on the surface and F on the surface; B on the surface and F in the air; B elsewhere and F in the subsurface; B elsewhere and F on the surface; and B elsewhere and F in the air. The addition of a shrub stratum in a shrubland community means there are 16 general ways in which wildlife can utilize those habitats. The addition of tree bole and tree canopy strata in a forest suggests that there may be as many as 36 combinations by which wildlife can utilize forests.

The numbers of strata available as wildlife habitat and the numbers of nonfish vertebrates breeding in those habitats increase as the complexity of habitat structure increases from grassland to forest and especially to riparian forest (Fig. 4). Riparian communities may maximize the number of strata available as wildlife habitat within a land section. Riparian communities vary in importance, however, depending on the number of strata actually present. A forest community present in an arid region because of subsurface moisture does not provide as many habitat use combinations for wildlife as does a wetland forest community where aquatic strata are also available.

Information about wildlife communities, organized in even this simplified manner, suggests the impacts that can be expected to occur if land changes affect the structure of vegetation. Spraying of sagebrush and chaining of pinyon-juniper, for example, destroy the structure of vegetative

Surface cover type	Strata									No. of potential breeding species
	BWC	WC	SWC	TSS	TS	SS	TB	TC	Total	
Riparian treeland	0	0	0	0	0	0	●	●	2-8	152
Riparian shrubland	0	0	0	0	0	●			1-6	99
Riparian grassland	0	0	0	0	●				1-5	81
Upland treeland with shrub midstory										
P.pine				●	●	●	●	●	5	124
Aspen				●	●	●	●	●	5	100
Upland treeland with no midstory				●	●		●	●	4	ND
Upland shrubland				●	●	●			3	86
Upland grassland				●	●				2	77
Consolidated substrate (rock)					●				1	ND

Fig. 4. The number of strata available as breeding habitat and the number of vertebrate species potentially breeding in those habitats. Closed circles indicate the strata that are present and open circles indicate additional strata that may be present in different types of surface cover. ND = no data.

communities and act to collapse somewhat complex habitats into the simpler form of grassland habitats. The quality of wildlife habitat in these areas (in terms of the diversity of the total wildlife community that can be supported on an area) is appreciably diminished by such actions.

If the general matrix discussed above is somewhat modified into a species-habitat matrix (Fig. 5), it becomes a useful tool in describing how wildlife species utilize the available strata of habitats. The division of the y-axis allows secondary consumers to be separated from primary consumers so that omnivores can be shown as competing with different species when in their two different consumer roles. We term the guild blocks, when modified to form the species habitat matrix (Fig. 5), "super cells" and base our guilding technology on this concept of super cells.

Species that feed on vegetation on the terrestrial surface and breed in an underground burrow (terrestrial subsurface), for example, would occupy super cell A, identified in Fig. 5. If those species are omnivorous and feed on both vegetation and insects on the terrestrial surface they would occupy super cells A and B in Fig. 5. Super cell A actually consists of 12 rows (Appendix I) and six columns (Appendix II) or 72 individual cells; super cell B consists of 8 rows (Appendix I) and six columns (Appendix II) or 48 indi-

vidual cells. A variety of species that use different food sources and breeding niches within these loci might thus be clumped within super cells A and B. The primary consumer activities of an omnivorous species may occur in super cells different from those of its secondary consumer activities.

The computer graphics presented in Figs. 6-8 are derived from the four statistical values ($\bar{x}$, $\bar{y}$, SD_x, SD_y) which are developed for each species occurring in a habitat. The graphics in Figs. 6-8 indicate ellipses of various sizes and shapes, representing the position or area each species occupies in the species-habitat matrix for a particular type of vegetation. The x-axis of the ellipse, within a particular type of vegetation, describes a single standard deviation of the one or several columns representing the appropriate breeding-niches for a species (Appendix II); the y-axis of the ellipse describes a single standard deviation of the one or several rows (Appendix I) representing the appropriate energy sources for that species. Although the program producing the computer graphics identifies the individual species described by a particular ellipse, that identification has been removed in Figs. 6-8 to simplify the presentation.

The increasing complexity of wildlife communities, as midstory and overstory strata become available, and

Energy source		Breeding habitat →	Bottom water column	Water column	Water surface	Terrestrial subsurface (3.1)	Terrestrial surface (3.2)	Shrub strata (3.3)	Tree bole (3.4)	Tree canopy (3.5)	Breeds elsewhere (4.0)
Secondary consumers	Air (2.3)										
	Tree canopy (2.25)										
	Tree bole (2.24)										
	Shrub strata (2.23)										
	Terr. surface (2.22)					B					
	Terr. subsurface (2.21)										
	Water surface (2.13)										
	Water column (2.12)										
	Bottom water column (2.11)										
Primary consumers	Tree canopy (1.25)										
	Tree bole (1.24)										
	Shrub strata (1.23)										
	Terr. surface (1.22)					A					
	Terr. subsurface (1.21)										
	Water surface (1.13)										
	Water column (1.12)										
	Bottom water column (1.11)										

Breeding habitat

Fig. 5. General appearance of the species-habitat matrix. Wildlife species that feed on vegetative materials on the terrestrial surface and reproduce in burrows or caves occupy super cell A, and wildlife species that feed on animal matter on the terrestrial surface and reproduce in burrows or caves occupy super cell B.

133
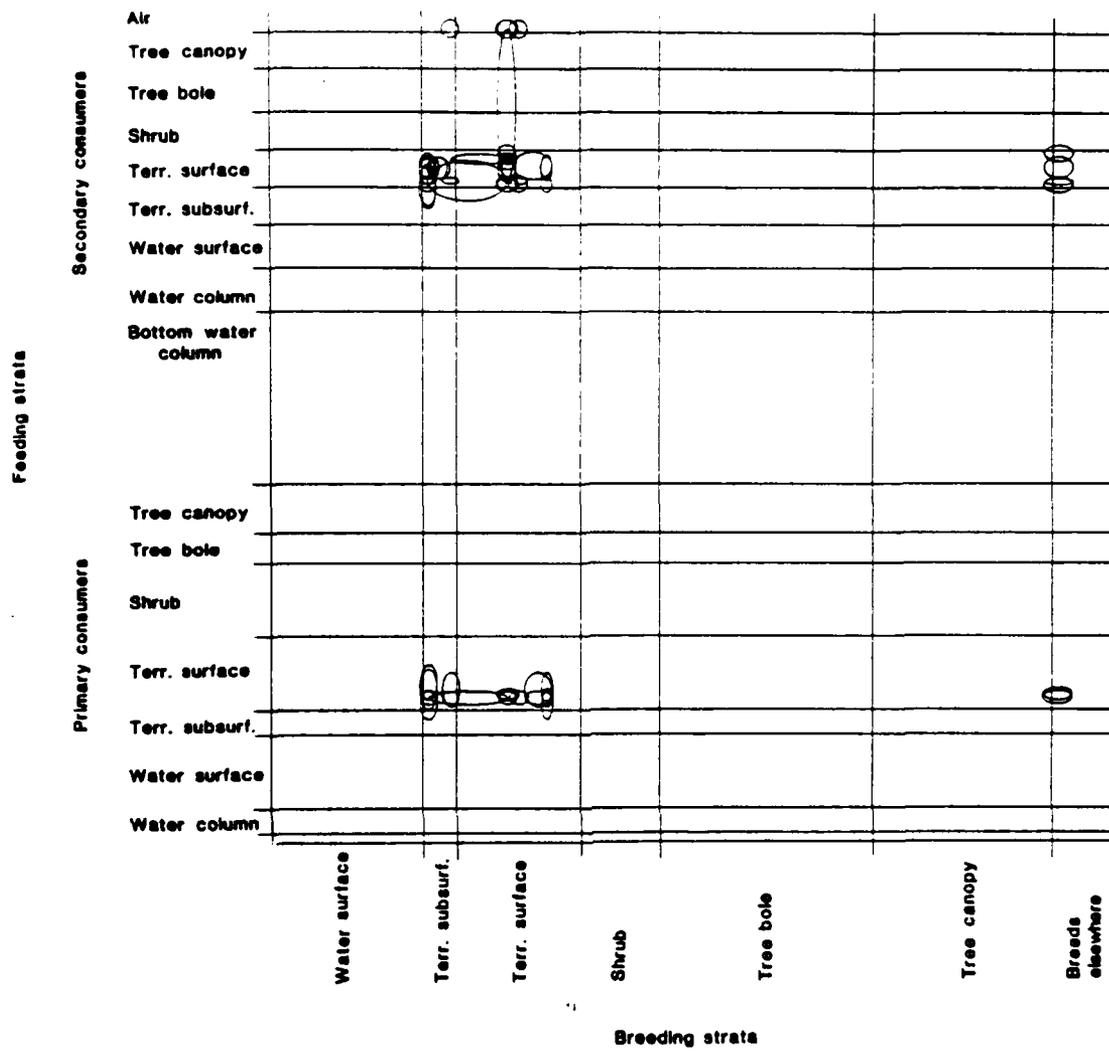
Fig. 6. The positions occupied by individual vertebrate species within the super cells of the species-habitat matrix for upland grassland habitats.

useful habitat is indicated in Figs. 6–8. This increasing complexity is a function of the availability of more strata, the increased number of species occurring in a given habitat, and the fact that some species will use a greater variety of strata when they are available.

The size of an ellipse within a habitat indicates the relative degree of specialization of a species and the shortest axis of the ellipse indicates whether greatest specialization occurs in requirements for breeding or feeding. Species represented by ellipses that are contained within a single habitat stratum can be expected to be adversely impacted by destruction of that stratum and favored by its enhance-

ment. The effects of managing strata on wildlife species can therefore be predicted from the graphics representations. For example, overgrazing on the terrestrial surface stratum, use of phytochemicals in sagebrush eradication, or broad-scale chaining of pinyon–juniper habitats would destroy habitats for species whose ecological requirements are summarized by small ellipses in the terrestrial surface or shrub strata of these respective types of habitat. Strata management, such as the retention of suitable tree boles or snags, may therefore benefit nesting species with requirements for that particular stratum.

Species represented by small ellipses within a single
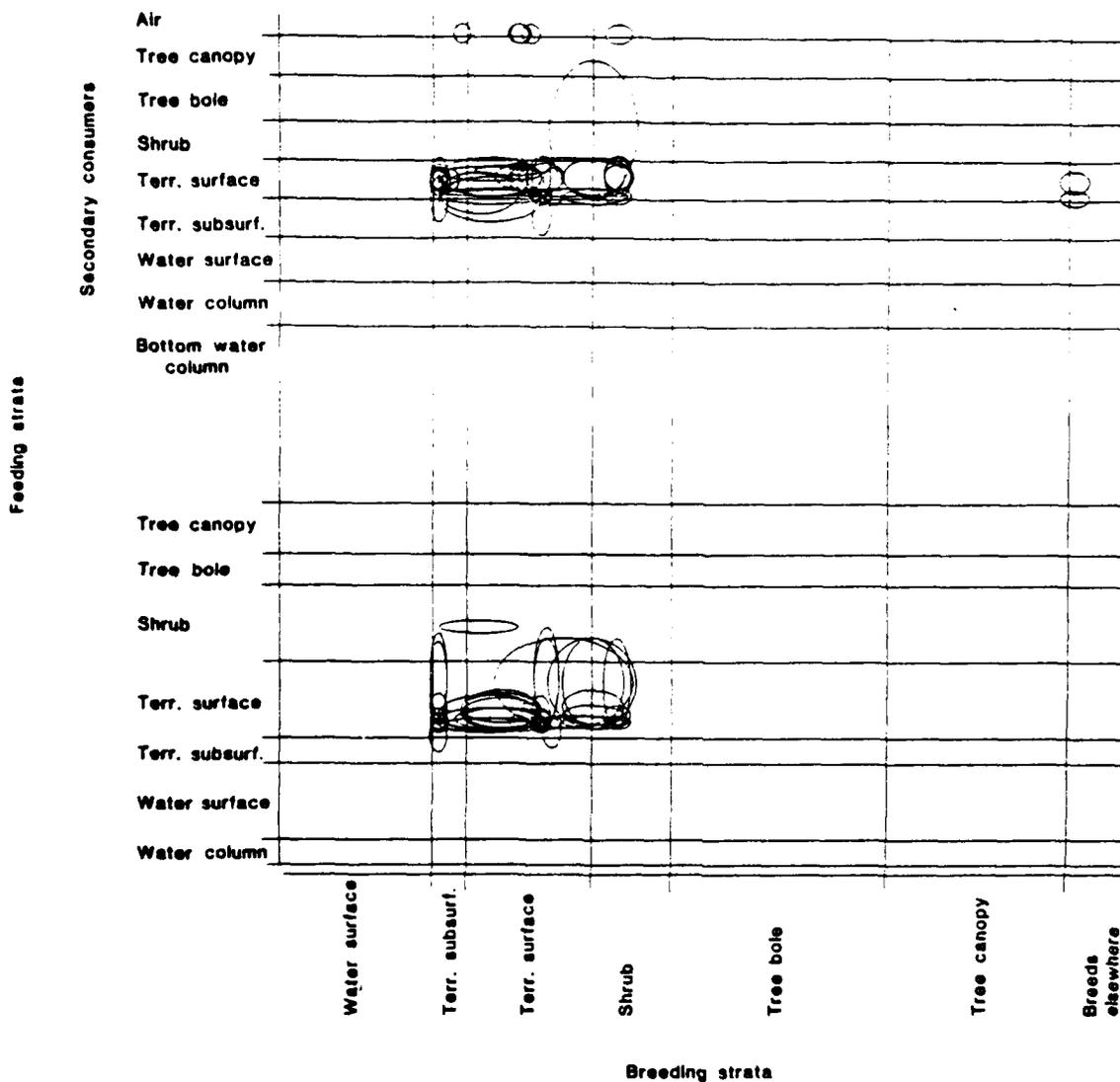
Fig. 7. The positions occupied by individual vertebrate species within the super cells of the species-habitat matrix for upland shrubland habitats.

stratum of habitat, where that stratum or habitat occurs in short supply, should be of special concern to planners and managers. These species may be candidates for threatened or endangered status in the future. Species represented by small ellipses in strata that occur in abundant habitat types would presumably be threatened only if adverse habitat impacts occurred on a wide scale.

The x-y coordinates describing the cells in the species-habitat matrix for the mature ponderosa pine community occupied by the Steller's jay are listed in Table 1 and the position of these cells in the species-habitat matrix is indi-

cated in Fig. 3. The cluster analysis routine of Rohlf et al. (1979) develops wildlife guilds from the types of information listed in Table 1 and Fig. 3. Groups of species are clustered together on the basis of the areas (determined by the means and variances of their x-y coordinates) each occupies in the species-habitat matrix. A group of species (I) that occupies the same (or nearly the same) group of cells within the species-habitat matrix are clustered together, and species that occupy groups of cells at varying distances from (I) in the matrix are clustered at varying distances from (I). Groups of species within a certain dis-

135
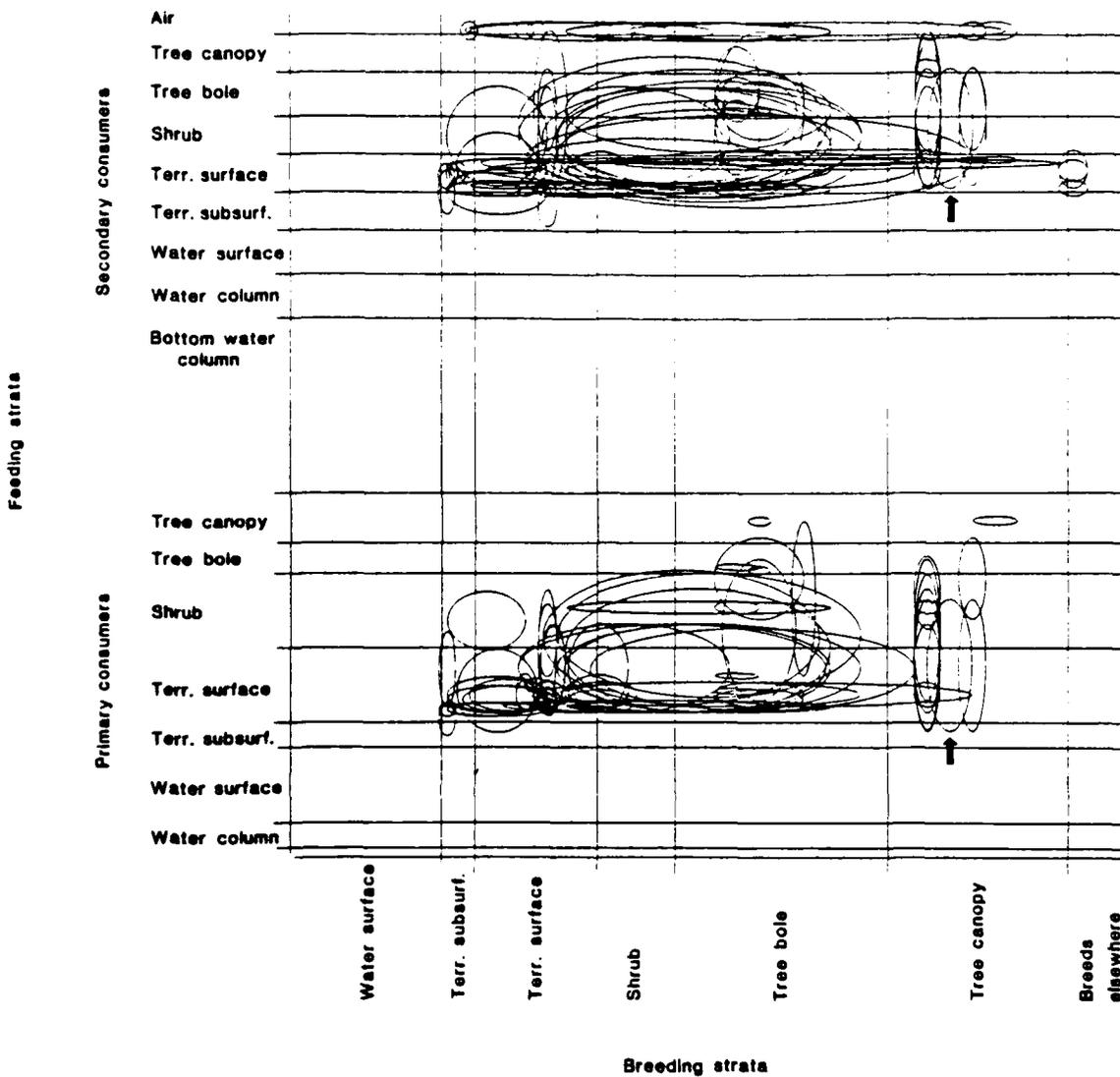
Fig. 8. The positions occupied by individual vertebrate species within the super cells of the species-habitat matrix for upland coniferous woodland habitats. The two ellipses identified by arrows represent the area within the species-habitat matrix occupied by Steller's jay (Table 1).

tance of each other (empirically determined by us not to exceed 3.6 units of Euclidean distance on the x-axis for the phenograms in Figs. 9–11) generally share the same combinations of super cells in fulfilling their breeding and feeding activities.

The splitting of the y-axis in the species-habitat matrix (Fig. 5) causes the cluster analysis routine to produce guilds of species that are either primary or secondary consumers (Figs. 9–11). The use of 3.6 units of Euclidean distance as a determinant for aggregating results from the cluster analysis into wildlife guilds produces groups of

species that tend to feed and breed within the same combination of super cells. The relationship between guilds and super cells that results from this mathematical model is strong: the regression equation (Table 3) is $\hat{Y}$ (number of guilds) = 1.13 times (the number of occupied super cells) − 6.24 (r = 0.99).

The actual development of wildlife guilds is illustrated in the following example. The ellipse plots developed for the primary consumers breeding in the tree canopy of a mature ponderosa pine community are represented in Fig. 12. These plots represent a subset of the ellipse plots

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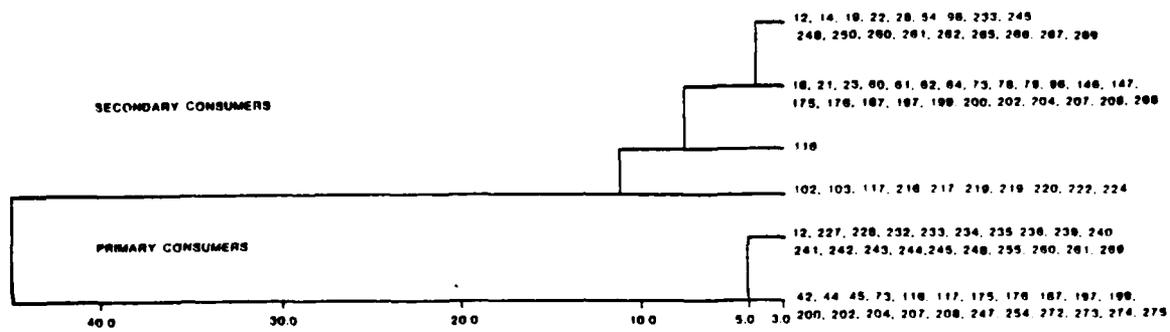
Fig. 9. Phenogram of vertebrate species potentially breeding in upland grassland habitats. R value of phenogram = 0.98. The species within the guilds can be identified from Appendix III. Units along abscissa are measures of Euclidean distances.
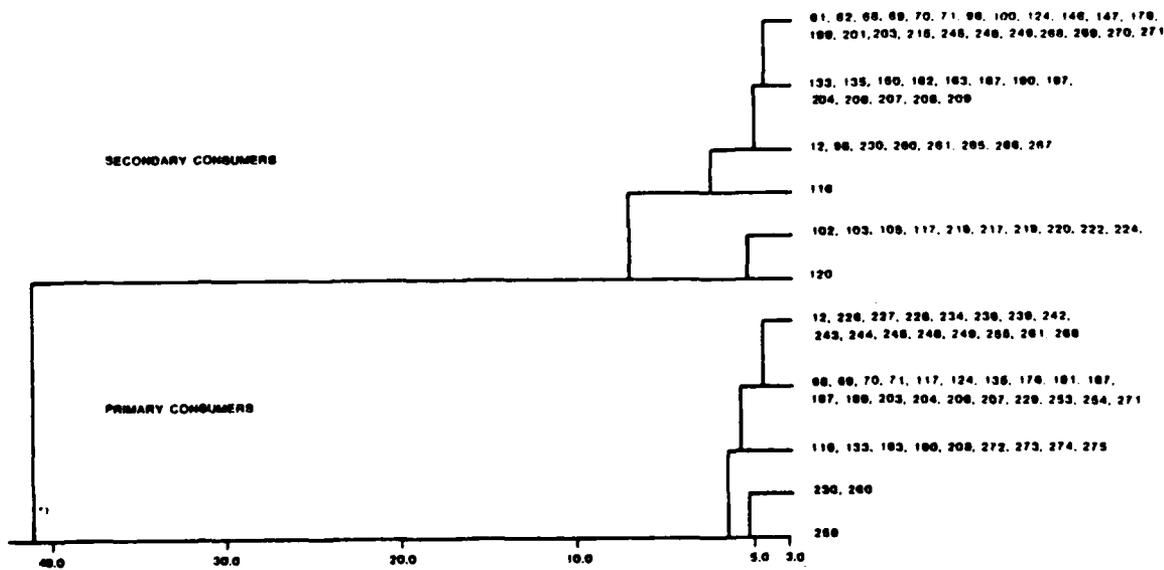

Fig. 10. Phenogram of vertebrate species potentially breeding in upland shrubland habitats. R value of phenogram = 0.98.

listed in Fig. 8. The cluster analysis routine disaggregated the 13 data sets represented by the 13 ellipses into the four guilds or groups of wildlife species also indicated in Fig. 12. The four groups of wildlife species represent that fraction of the phenogram or dendrogram distinguished by a bracket in Fig. 11. The four guilds represent groups of wildlife species that share the way they utilize the strata provided by the ponderosa pine woodland as feeding and breeding habitats.

The actual use of super cells for feeding and breeding habitats for all the primary consumers in the ponderosa pine forest is represented in Fig. 13. The letters indicating the positions occupied by each guild in the matrix of Fig. 13 identify the guild in the dendrogram of Fig. 11. The wildlife species represented by the guilds depicted in

Figs. 11 and 13 can be identified from Appendix III. Guild R, for example, in Figs. 11, 12, and 13 is composed only of the mourning dove which breeds in the tree canopy and feeds on seeds on the terrestrial surface. Guild S consists of eight species (including the Steller's jay) which breed in the tree canopy and forage on the terrestrial surface, in the shrub strata, and in the tree canopy. This variability in foraging strata is obvious in the large ellipses (large SD$_v$) for those species evident in Figs. 8 and 12. Guild T in Figs. 11, 12, and 13 consists of the ruby-crowned kinglet, evening grosbeak, and red crossbill which breed in the tree canopy and which forage within the shrub and tree canopies. Guild U in Figs. 11, 12, and 13 is composed only of the western wood peewee which breeds and forages only in the tree canopy. The other 17 groups or guilds of
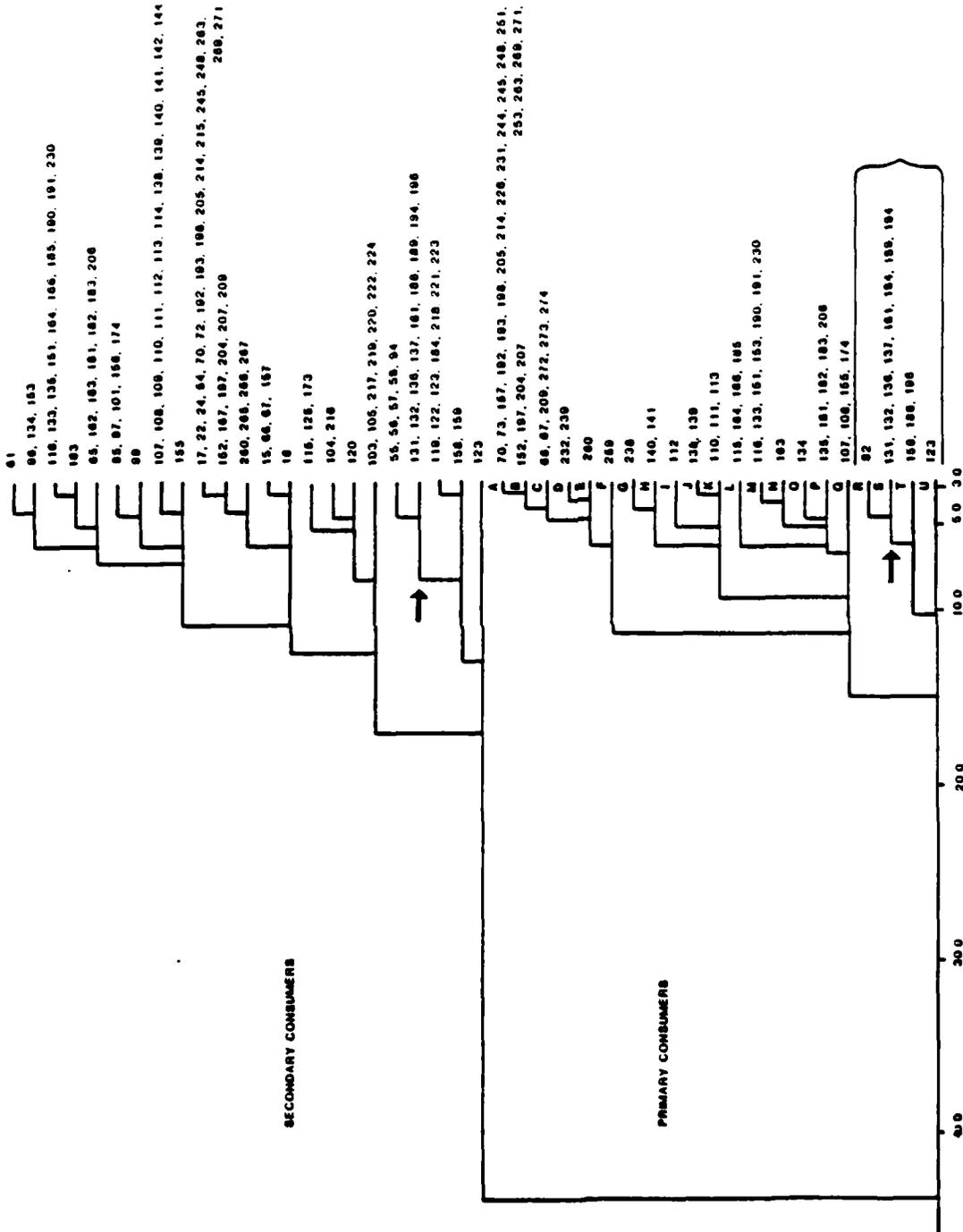
Fig. 11. Phenogram of vertebrate species potentially breeding in upland coniferous woodland habitats. R value of phenogram = 0.96. Steller's jay is a member of each of the two guilds which are identified by arrows (see text for explanation). Units along abscissa are measures of Euclidean distances. Guilds identified by brackets are described in Fig. 12. Guilds identified by letters are listed on Fig. 13

Table 3. Relation[a] between number of potential breeding species, number of occupied super cells, and number of wildlife guilds in seven habitat types.

Community type	No. potential breeding species	No. occupied super cells	No. wildlife guilds
Upland grassland	77	9	6
Riparian grassland	81	24	27
Upland shrubland	86	19	11
Riparian shrubland	99	38	32
Upland coniferous woodland (ponderosa pine)	124	44	44
Upland deciduous woodland (aspen)	100	41	39
Riparian woodland	152	68	73

[a]Number of guilds (Ŷ) = 1.13 (number of super cells) - 6.24, r = 0.99; number of guilds (Ŷ) = 0.78 (number of breeding species) - 47.43, r = 0.94; number of super cells (Ŷ) = 0.69 (number of breeding species) - 35.87, r = 0.95.

wildlife species acting as primary consumers and identified by letter in Figs. 11 and 13 also occupy unique combinations of cells within the species-habitat matrix. The seven species comprising Guild M are generalists breeding and feeding in a variety of strata. Guild N represents the ubiquitous starling that occupies a unique combination of strata for foraging and breeding habitat and Guild I is composed of the hairy woodpecker which breeds in the tree bole and feeds in the tree canopy.

The position of the Steller's jay in the dendrogram of Fig. 11 is represented by two arrows. The structure of the primary consumer guild occupied by the Steller's jay has been described above. The Steller's jay also may act as a secondary consumer and in this capacity shares a guild with the gray jay, pinyon jay, Clark's nutcracker, cedar waxwing, evening grosbeak, Cassin's finch, pine siskin, and red crossbill. The nine birds all consume insects and most (except the evening grosbeak and red crossbill) do some foraging for insects on the ground surface. Except for the pinyon jay, all may also forage for insects in the tree canopy (Table 4). Some variability occurs in food habits,

Area described by
X - Y coordinate data
from Fig. 8

Guilds formed from
X - Y coordinate data

Guild R —— Mourning dove (92)

Guild S ——
Gray jay (131)
Steller's jay (132)
Pinyon jay (136)
Clark's nutcracker (137)
Cedar waxwing (161)
Western tanager (184)
Cassin's finch (189)
Pine siskin (194)

Guild T ——
Ruby-crowned kinglet (159)
Evening grosbeak (188)
Red crossbill (196)

Guild U —— Western wood pewee (123)
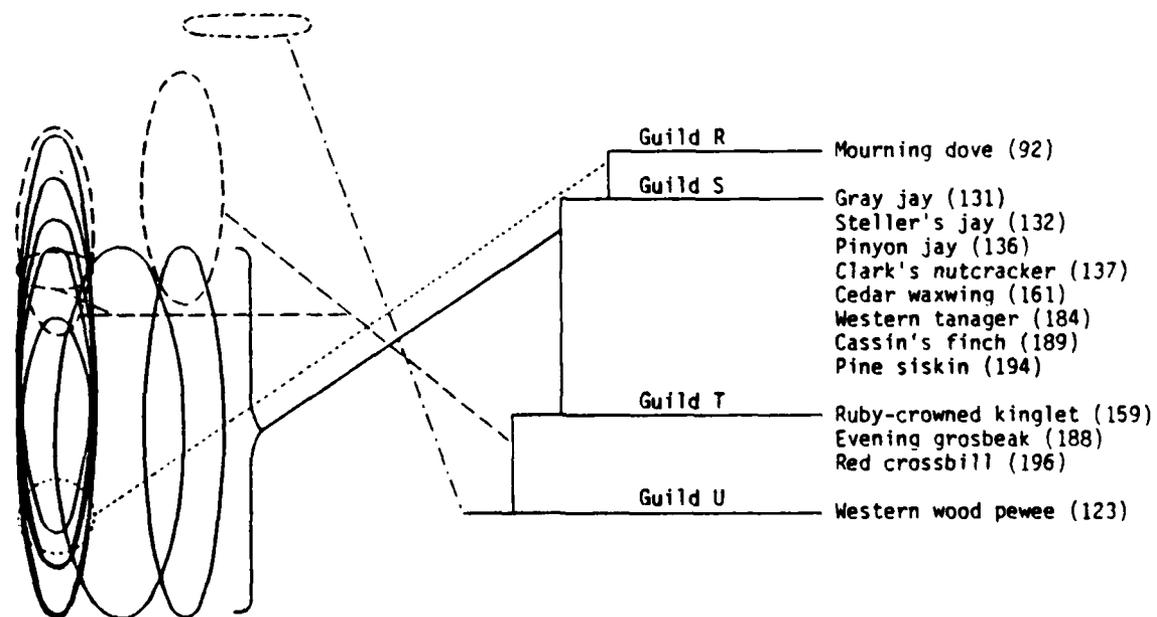
Fig. 12. The ellipse plots correspond to those on Fig. 8 which represent the data for primary consumers that breed in the tree canopy and feed on the terrestrial surface, shrub, tree bole, and tree canopy strata. The cluster analysis routine disaggregates these 13 data sets into the four guilds which are identified by the bracket in Fig. 11.

Upland coniferous woods

Primary consumers only

Feeding strata

Tree canopy
Tree bole
Shrub
Terrestrial surface
Terrestrial subsurface

Terrestrial subsurface | Terrestrial surface | Shrub | Tree bole | Tree canopy | Breeds elsewhere

Breeding strata
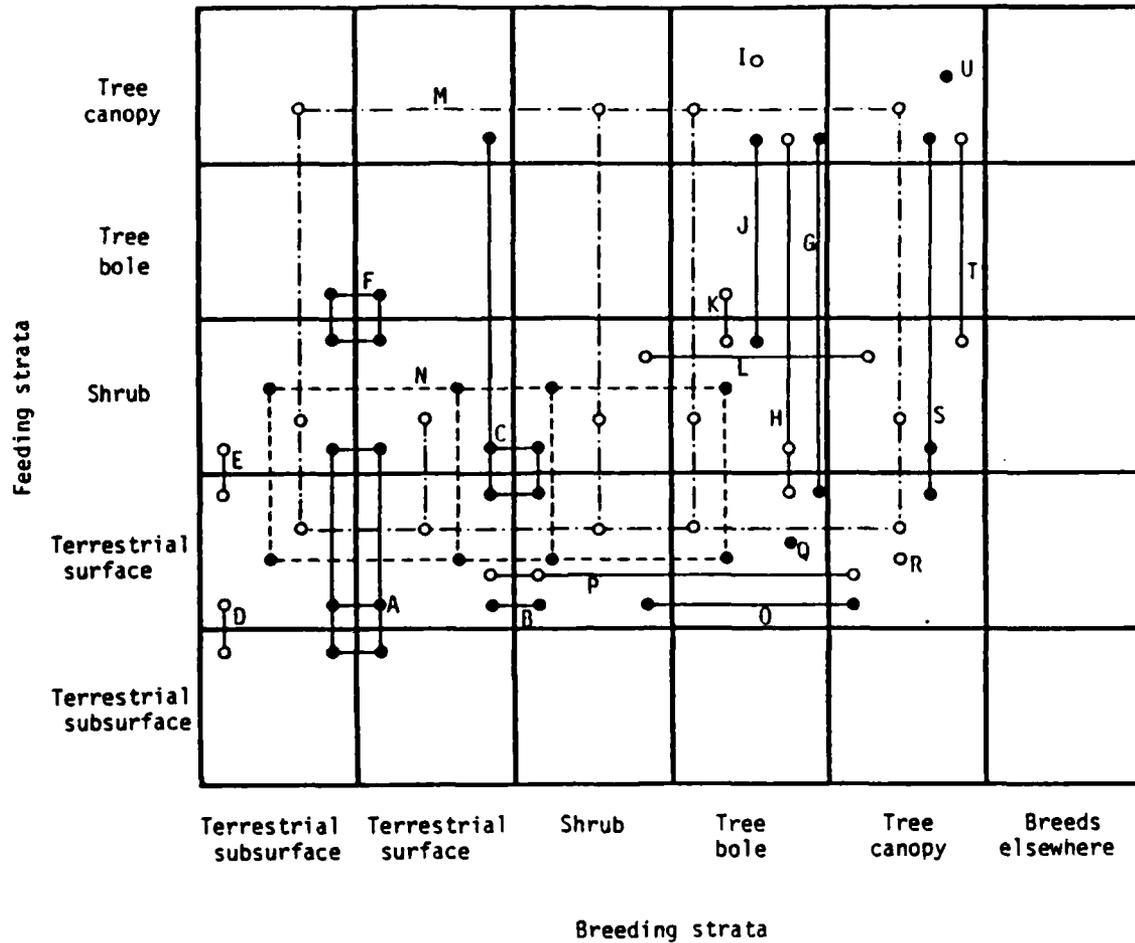
Fig. 13. The guilds of primary consumers indicated in Fig. 11 occupy various combinations of super cells. The letters identifying a guild are also listed on the phenogram in Fig. 11 so both the species forming each guild and the super cells used by each guild can be identified. Different symbols are used to simplify the figure.

however, because the Clark's nutcracker and the gray jay supplement their diets with small mammals and amphibians from the ground surface and with the contents of bird nests found in the tree canopy.

The wildlife guilds defined by the application of cluster analyses possess biological attributes that make the results from the model seem attractive. Species comprising wildlife guilds should be restricted to individual super cells, or similar combinations of super cells, if they are to use environmental resources in a similar manner. The complexity of a biological community in terms of the number of guilds should increase as the number of super cells increases in the habitat. In addition, the close association of wildlife guilds with super cells suggests a basis for predicting impacts on the wildlife community caused by changes in the structure (guild blocks) of vegetative communities. This last generalization is described here.

The structure of the species-habitat matrix suggests that the number of super cells will increase at a geometric rate

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Table 4. *Composition of two guilds containing Steller's jay in a community of mature ponderosa pine. All species feed in the tree canopy.*

Vertebrate species[a]	Strata[b] where feeding occurs
Primary Consumer	
Pinyon jay	TS. TC
Cedar waxwing	TS. SS. TC
Cassin's finch	TS. SS. TC
Clark's nutcracker	TS. TC
Gray jay	TS. TC
Steller's jay	TS. TC
Western tanager	TS. SS
Pine siskin	TS. SS. TC
Secondary Consumer	
Pinyon jay	TS
Clark's nutcracker	TS. TB. TC
Cedar waxwing	TS. TC
Gray jay	TS. TC
Steller's jay	TS. TC
Cassin's finch	TS. SS. TC
Pine siskin	TS. SS. TC
Evening grosbeak	SS. TC
Red crossbill	SS. TC

[a]See Appendix III for scientific names.
[b]TS = terrestrial surface. SS = shrub strata. TB = tree hole. TC = tree canopy.

as strata are added to vegetative cover types. Numbers of guilds also seem to increase at a geometric rate, whereas the number of wildlife species increases in a linear manner as strata are added to vegetative cover types (Table 3). The increase in the number of guilds is a function of both the increased opportunities provided by the addition of guild blocks and the increased opportunity for "generalists" that can utilize unique combinations of guild blocks as wildlife habitat. These "generalists" are depicted as "single member guilds" in Figs. 10 and 11. These "generalists" are fairly common in the upland coniferous woodland community (Fig. 11).

Six wildlife guilds were identified for upland grassland (Fig. 9), 11 for the sagebrush steppe (Fig. 10), and 44 as possibly occurring in the ponderosa pine community. Obviously, the number of groups of species that utilize habitat resources in about the same manner increases as the resource opportunities increase with the addition of strata and guild blocks in a habitat. Some of the wildlife guilds identified in Figs. 9–11 and Appendix III may seem to be unlikely guild partners. This guilding technique, however, is intended to link wildlife species with the structure of vegetation and to group species that share dependencies on vegetation of similar structure. These wildlife guilds may include animals from different taxonomic classes and of different biomasses. The animals form a guild if they utilize similar food sources and breeding strategies even

though one animal may require grams of a particular plant food, whereas another may require a kilogram of that food. Changes that impact that food will obviously affect both species.

Several techniques have been used to disaggregate groups or guilds of wildlife species to describe particular ecological niches or to describe in detail the unique foraging or reproductive strategies used by a species. Principal Component Analysis (PCA), for example, has been used to determine how guild members actually partition the resources within a guild block. For example, PCA has been used by Anderson and Shugart (1974) to describe the selection of habitat by birds in a deciduous forest in Tennessee. by Rotenberry and Wiens (1980) to determine the effects of vegetation structure on breeding bird populations in steppe habitats of North America. and by Niemi and Pfannmuller (1979) to describe the niche structure for 21 bird species in northeastern Minnesota.

Discussion

The guilding technique is a way to organize and analyze information about wildlife species to provide insight about the structure of wildlife communities under both present and proposed habitat conditions. The development of wildlife guilds provides an excellent model from which to select wildlife species to accomplish a variety of wildlife studies. In addition, wildlife guilds are useful for interpreting the results of inventories and assessments, in performing integrated assessments and management of natural resources, and in forecasting the impact of habitat change on wildlife. Some of these potential applications are described here in detail. The applications are built on two assumptions which are in addition to those six described in the introduction to this paper.

Assumption 7

Guilds of vertebrate animals are, because of the nature of the species-habitat matrix, closely associated with guild blocks. Consequently, it is possible to predict impacts on the wildlife community resulting from changes that will modify the quantity and quality of guild blocks in the vegetative community.

Integrated Management of Renewable
Natural Resources

The association of wildlife species with vegetative structure when using the species-habitat matrix provides a common denominator with which other natural resources can be considered in the integrated analyses of natural resources. Fish and wildlife species are associated with various strata in the guilding process and many other natural resource products can also be considered as strata products. For example, strip-mining affects surface and subsurface layers, most agriculture uses the surface strata,

and timber management manipulates the tree hole and tree canopy layers. The impact of various land-management activities on fish and wildlife resources can be predicted from computer simulations that modify energy sources and breeding niches (rows and columns of the species-habitat matrix, Appendices I and II) in the affected strata. Computer simulations can thus display various management options so that development can occur in ways that reduce impacts on wildlife guilds.

Systems Approach for Assessing Wildlife Habitat in the Decision Process

The utility of any habitat evaluation effort is determined by its effectiveness in the decision-making process. The technique described in this paper has relevance to land-use management decision-making because it relates the wildlife community to the structure of vegetative surface cover, which can be controlled through management and predicted through time. This methodology deals with the total wildlife community and can be used to predict changes from established base-line conditions which determine the wildlife guilds present at a specific point in time. Wildlife guilds potentially present in the future can be predicted by establishing species-habitat matrices for the seral stages of surface cover types predicted to be present at those future dates. A comparison of the product of area times guilds times years with base-line conditions represents gains or losses associated with changes in land use and is essentially an assessment of potential impacts.

A conceptual model, developed by Erickson et al. (1980), for assessing wildlife–land-use relationships in the decision-making process is reproduced in Fig. 14. Abiotic, biotic, and human conditions produce the existing wildlife habitat on a site. Areas of different cover types on a development site can be calculated (Table 5) and the guilds that occur in those cover types can be determined. The determination of guilds actually present on a site is made from on-site surveys which provide faunal lists for the different areas of existing wildlife habitat. The species actually present are compared with those species forming the wildlife guilds to determine the guilds actually represented on-site.

Proposed land-use changes will impact the structure of vegetation so that areas of different types of vegetation likely to be present at different time intervals during the life of the proposed project can be predicted (Table 5). The predicted wildlife community (number of guilds) at any time during the project's life can be developed from species-habitat matrices developed for the vegetative types presumed present after development.

The simple calculation of multiplying present hectares by present guilds and future hectares by future guilds (Table 5) illustrates how changes in the total wildlife community can be predicted on the basis of the impacts of proposed land-use options on vegetative surface cover within a land area. These changes can be predicted for a single point in time or for the life of a project.

Assumption 8

Vertebrate species may be present in a habitat if suitable environmental factors, including food sources and breeding niches, are present. The greater the number of suitable environmental factors present in a habitat, up to some point, the greater the potential species richness that may occur in that habitat.

Food sources and breeding niches itemized in Appendices I and II and included in the species-habitat matrix (Fig. 5) are among the most important environmental factors determining the suitability of a habitat for a species. The presence of food sources and breeding niches within guild blocks and the addition of guild blocks to habitat obviously affect species richness. The impact on species richness of modifying food sources (rows) within the species-habitat matrix can be simulated with the data sets used to develop the relationships in Figs. 9–11. For this illustration, the impact of moderate overgrazing is simulated by deleting rows 53–56 and 65–70 (Appendix I) from the computer model. This condition would be realized if essentially all current annual growth in the terrestrial surface strata and in the shrub strata had been removed by grazing. Although representatives of all the potential guilds remain in upland grassland, upland shrub (sagebrush), and upland coniferous woodland (ponderosa pine) habitats, following the simulation, the number of primary consumers in each of the three vegetative types is reduced (Table 6). The specialists requiring herbaceous, forb, or deciduous browse in the surface or shrub strata disappear from these three cover types when the appropriate cells disappear.

Predictive associations can be developed that relate species richness, the total number of vertebrate species on an area, to the number of guild blocks and the structure of vegetation within the strata of different cover types. Such a model is described by Short (1982).

The habitat-gradient model states that of two habitats with the same basic vegetative structure (and thus with the same number of guild blocks), the habitat with greater vegetative density, greater equitability of cover between strata, greater block size, and more persistent vegetation, will have more species and presumably more of the possible guilds that can occur in the habitat type. Thus guilds present on an area within a particular potential vegetation type can be used as an assessment of habitat quality. The habitat-gradient model neither predicts the individual species likely to be present nor the actual guild structure of the community likely to occur on that habitat. Identification of individual species occurring on a site is a product of animal inventory information. A comparison of animals found on a site with lists of species constituting potential guilds for that habitat type is the best way to determine the actual guilds occurring in an area.

The habitat-gradient model can also be derived from interpreted aerial photography (Short 1982). An area to be characterized is first subjected to an on-site evaluation to
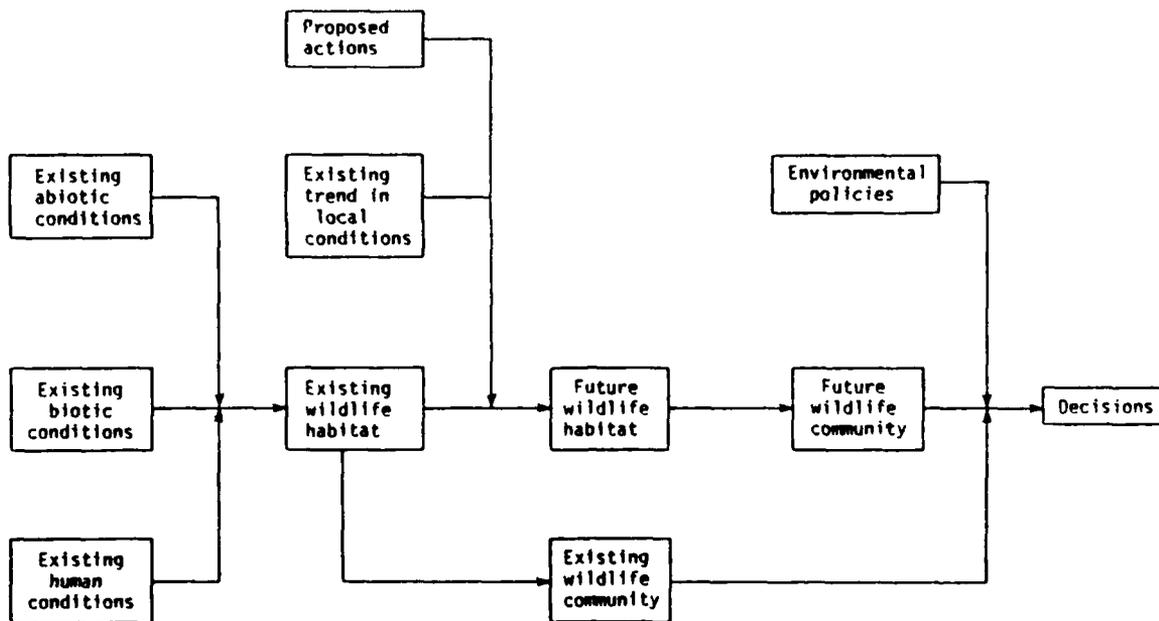
Fig. 14. A systems approach to the assessment of wildlife–land-use relations and the decision-making process (after Erickson et al. 1980).

Table 5. *Calculation of predicted change in the wildlife community caused by modification of vegetation cover types resulting from proposed land-use actions.*

| | Hectares in block | | Guilds in habitat | | Community comparison | |
| | | | | | Present guilds × hectares | Proposed guilds × hectares |
Polygon cover type	Present	Proposed	Present	Proposed		
A	200		30		6,000	
B	500	300	20	20	10,000	6,000
C	100		15		1,500	
D	100		12		1,200	
E	100		10		1,000	
F		700		15		10,500
Total					19,700	16,500

Change in composition and size of wildlife community associated with land use change = 19,700 − 16,500/19,700 = 16.2% = the potential reduction in wildlife values.

Table 6. *Impacts of heavy grazing on guilds and number of primary consumers in three types of upland vegetative cover.*

| | Nongrazed condition | | Heavily grazed condition | |
| | No. of potential guilds | Total no. primary consumers | No. of potential guilds present | Total no. primary consumers |
Vegetation cover type				
Upland grassland	2[a]	42	2	12
Upland shrubland	6	48	6	33
Upland coniferous woodland	21	76	21	66

[a]Impact is calculated only for guilds of primary consumers.

develop prediction equations between overstory density and the density of cover in the midstory and understory. Aerial photographs are then differentiated into polygons on the basis of the structure and density of the overstory so that, using the prediction equations, a representation of the vertical profile of each polygon is formed. A habitat characterization value is then developed for each polygon using the same structural parameters (number of guild blocks, vegetative density, equitability of cover between strata, etc.) used in predicting species-richness from on-site assessments. The habitat characterization value of a polygon multiplied by the area of that polygon and summed for all the polygons within the area being characterized represents the numerator of a ratio whose denominator is the maximum characterization value that can be expected within that potential natural vegetation type. The greater the ratio, the greater the presumed species-richness in the area and the greater the presumed area × guilds value for the characterized area.

Habitat evaluation using guilds is a measure of total guilds that have members which apparently find a piece of land to be adequate habitat. This type of analysis allows the animal to determine whether a habitat adequately provides for its life requirements. The analysis does not determine how adequate the habitat is for a particular species, nor does it determine whether nonhabitat-related factors are responsible for the absence of a species from an area. The assumption is that a member of a wildlife guild will be present in a habitat if that habitat provides suitable life requirements for a guild member. If the first of two pieces of land, with the same possible guild structure, sustains representative species of only 25% of the guilds that can occur in that vegetative community, then that land is of lesser quality to the total wildlife community than is the second piece of land sustaining representatives of 75% of the guilds that can occur in that vegetative community.

Lists of guilds found on an area in a particular vegetative type can be compared with lists of guilds that can theoretically occur in that potential vegetation type. The determination of why guilds are apparently missing from an area can be a diagnostic exercise. Is a guild missing because of some structural deficiency (affecting food sources and breeding niches) in a guild block? Can some remedial management practice be exercised to correct structural deficiencies so that habitat for particular guilds can be enhanced?

The Habitat Evaluation Procedures (HEP; U.S. Fish and Wildlife Service 1980) will accept a measurement of habitat suitability that is a ratio of guilds observed in a cover type divided by the numbers of guilds that can occur in that potential vegetative type. The bound of potential vegetation thus provides a standard of comparison for all those cover types within a potential vegetation type. The habitat suitability value provides a measure of habitat quality for base-line conditions. For future conditions, predicted wildlife guilds can be simulated from data developed from the species-habitat matrices for the vegeta-

tive cover types hypothesized present at some future time, t. The denominator to determine future habitat quality remains the same because the potential natural vegetation remains the same. The numerator at time t is determined from the guilds predicted present at t. Predicted guilds are determined from the presumed vegetative cover type and its structure at time t. The simulation to determine the wildlife community present at t may include any modifications to strata, and rows and columns within strata, for the species-habitat matrix describing the cover type presumed present at time t. Multiple future conditions can be simulated for the decision-maker, to determine the effects of different management options on habitat quality at time t. The ratio developed from predicted guilds and the standard of comparison produces a measure of future habitat quality.

The advantages of using the guilding technique in HEP are that guilding provides a measure of habitat quality pertinent to the total wildlife community on an area, and that simple faunal surveys can provide the field data for determining base-line habitat quality.

Conclusions

We have described a technique for associating wildlife species with the structure of wildlife habitat so a variety of computerized analyses can occur to help predict impacts on wildlife caused by changes in the structure of habitat. The concepts developed in this paper were developed with a data base formulated for 275 wildlife species occurring in the eastern ponderosa pine type of forest (Küchler 1964, type 16) in southeastern Montana and northeastern Wyoming. Our technique is based on the assumption that a wildlife species can be categorized as occupying a discrete area within a two-dimensional "species-habitat" matrix. Food sources and breeding niche requirements make up the two axes of the species-habitat matrix and numeric values identify the cells representing the food sources and breeding niche requirements necessary for each wildlife species. A variety of statistical analyses can be accomplished on the areas (combinations of cells) occupied by different wildlife species so that a description of the structure of the wildlife community within a habitat type can be developed. The assumptions made in the development of the species-habitat matrix are included in the text.

The models produced in the present study indicate that (1) the species-habitat matrix provides a useful way to order wildlife information, (2) the statistical analyses provide a structuring of the wildlife community that is biologically reasonable, and (3) a variety of management needs are served in a unique way because the analyses pertain to the total wildlife community. In particular, the computer graphics illustrate, as expected, the complexity of the wildlife community that can occur as guild blocks are added to surface cover, and results from the cluster analyses describe, as expected, the increase in numbers of

wildlife guilds that occur as guild blocks are added to wildlife habitat.

The greatest difficulties in working with our guilding technique are associated with developing the data base to drive the guild analyses. Difficulties occur because wildlife species have not historically been associated with vertical strata in the environment (an important subdivision within the species-habitat matrix). We believe this is an imprecision in the quality of natural history information (field biologists have not historically associated species with strata), rather than a flaw in the design of the species-habitat matrix. The correct positioning of wildlife species within vertical strata requires expert judgment even though food habit and breeding niche requirements are among the best known information about individual species. A second problem encountered in building the data base is the determination of "normal" and "abnormal" food habits and breeding activities. We consider "abnormal" feeding and breeding information to be those exceptions that are so unusual and occur so rarely as to be noteworthy events. Such noteworthy events are not considered in the development of the species data base.

The suggested application of the principles determined from the guilding model is presumed and not proven. The determination of the utility of the proposed applications must wait until an applications study, presently under way, is completed. Still we can conclude that the ability to associate wildlife guilds with the structure of habitat allows good predictions to be made about the impacts of habitat change on the structure of the wildlife community, and that wildlife guilds actually occupying an area compared with the standard guild structure that can occupy an area may possibly be a useful measure of habitat quality. This measure compares the structure of the actual wildlife community with the structure of the wildlife community that would potentially occupy the area. The standard guild structure is determined for the climax community of the potential natural vegetation that can occur on an area and the actual guilds present on the area are determined by comparing species found on an area with lists of species comprising the guilds that can occur on the area. An additional utility of the guilding technique is that the structure of the wildlife community present at some future time can be simulated if the structure of the vegetation community present at the future time can be hypothesized. This capability should enhance the assessment of impacts of habitat change on the wildlife community.

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Appendix I

Y-coordinate Numbers (Left-hand Column) and the Corresponding Food Source by Strata (Right-hand Column) Used in the Determination of Wildlife Guilds

1.0 Primary Consumers

  1.1 Feeds on vegetation in aquatic systems

    1.11 Feeds on vegetation at bottom of water column (substrates are under water columns >25 cm deep)

Natural reef
001	Detritus (organic)
002	Plankton
003	Diatoms (encrusting on bottom substrate)
004	Filamentous algae
005	Rooted vascular plants
006	Other (e.g., parts of terrestrial rooted plants)

Artificial reef (man-made structure)
007	Detritus (organic)
008	Plankton
009	Diatoms (encrusting on bottom substrate)
010	Filamentous algae
011	Rooted vascular plants
012	Other (e.g., parts of terrestrial rooted plants)

Consolidated bottom
013	Detritus (organic)
014	Plankton
015	Diatoms (encrusting on bottom substrate)
016	Filamentous algae
017	Rooted vascular plants
018	Other (e.g., parts of terrestrial rooted plants)

Unconsolidated bottom
019	Detritus (organic)
020	Plankton
021	Diatoms (encrusting on bottom substrate)
022	Filamentous algae
023	Rooted vascular plants
024	Other (e.g., parts of terrestrial rooted plants)

Aquatic bed
025	Detritus (organic)
026	Plankton
027	Diatoms (encrusting on bottom substrate)
028	Filamentous algae
029	Rooted vascular plants
030	Other (e.g., parts of terrestrial rooted plants)

    1.12 Feeds on vegetation within water column (i.e., vegetation in water >25 cm below the surface)
031	Detritus (organic)
032	Plankton
033	Diatoms (encrusting on protruberances)
034	Filamentous algae (extending into column)
035	Rooted vascular plants (extending into column)
036	Other (e.g., parts of terrestrial rooted plants)

1.13 Feeds on vegetation at surface of water column (includes vegetation at shoreline or under shallow water [≤25 cm deep], in open water [≤25 cm deep], and on vegetation extending up to or through surface waters)

037	Detritus (organic)
038	Plankton
039	Diatoms (encrusting on protruberances)
040	Filamentous algae
041	Floating vascular plants
042	Rooted herbaceous vascular plants (at surface)
043	Rooted woody vascular plants (at surface)
044	Rooted herbaceous vascular plants (through surface)
045	Rooted woody vascular plants (through surface)
046	Moss (at water-land interface)
047	Other (e.g., parts of terrestrial woody plants)

1.2 Feeds on vegetation in terrestrial systems

1.21 Terrestrial subsurface (to 10 cm below apparent surface)

048	Fungi
049	Roots, tubers, and rhizomes of herbaceous plants
050	Roots, tubers, and rhizomes of woody plants
051	Other plant materials

1.22 Terrestrial surface (from 10 cm below apparent surface to 0.5 m above apparent surface)

052	Fungi
053	Grass and grasslike leaves and stems (including rootstock)
054	Grass and grasslike flowers and fruits
055	Forb leaves and stems (including rootstock)
056	Forb flowers and fruits
057	Deciduous shrub leaves and fruit (seeds) on ground (and leaves and fruit of deciduous supine shrubs)
058	Evergreen shrub leaves and fruit (seeds) on ground (and leaves and fruit of evergreen supine shrubs)
059	Deciduous tree leaves and fruit (seeds) on ground
060	Evergreen tree leaves and fruit (seeds) on ground
061	Roots, twigs, and bark of woody stems (extending into higher strata)
062	Cactus stems and pads
063	Cactus flowers and fruit

1.23 Shrub strata (from 0.5 to 8.0 m above apparent surface)

064	Fungi
065	Grass and grasslike leaves and stems (extending into shrub strata)
066	Grass and grasslike flowers and fruit (extending into shrub strata)
067	Forb leaves and stems (extending into shrub strata)
068	Forb flowers and fruit (extending into shrub strata)
069	Leaves and twigs (including cambium) of deciduous woody shrubs
070	Flowers and fruit of deciduous woody shrubs
071	Leaves and twigs (including cambium) of evergreen woody shrubs
072	Flowers and fruit of evergreen woody shrubs
073	Parasitic or epiphytic plants
074	Cactus stems and pads
075	Cactus flowers and fruit

1.24 Tree boles

076	Fungi
077	Tree sap
078	Tree cambium
079	Cactus stems and pads
080	Cactus flowers and fruit

1.25 Tree canopy

081	Fungi
082	Leaves and twigs of deciduous trees
083	Flowers, fruits, and seeds of deciduous trees
084	Leaves and twigs of evergreen trees
085	Flowers, fruits, and seeds of evergreen trees
086	Leaves and twigs of lianas
087	Flowers, fruits, and seeds of lianas
088	Parts from parasitic or epiphytic plants

2.0 Secondary Consumers

2.1 Feeds on animal matter in aquatic systems

2.11 Feeds on animal matter at bottom of water columns (substrates are under water columns > 25 cm deep)

Natural reef

089	Zooplankton
090	Arthropods
091	Other invertebrates (includes mollusks)
092	Fish (eggs, fry, adults)
093	Amphibians (eggs, juveniles, adults)
094	Reptiles (eggs, juveniles, adults)
095	Birds
096	Mammals
097	Scavenger (carrion)

Artificial reef (man-made structure)

098	Zooplankton
099	Arthropods
100	Other invertebrates (includes mollusks)
101	Fish (eggs, fry, adults)
102	Amphibians (eggs, juveniles, adults)
103	Reptiles (eggs, juveniles, adults)
104	Birds
105	Mammals
106	Scavenger (carrion)

Consolidated bottom

107	Zooplankton
108	Arthropods
109	Other invertebrates (includes mollusks)
110	Fish (eggs, fry, adults)
111	Amphibians (eggs, juveniles, adults)
112	Reptiles (eggs, juveniles, adults)
113	Birds
114	Mammals
115	Scavenger (carrion)

Unconsolidated bottom

116	Zooplankton
117	Arthropods
118	Other invertebrates (includes mollusks)
119	Fish (eggs, fry, adults)
120	Amphibians (eggs, juveniles, adults)
121	Reptiles (eggs, juveniles, adults)
122	Birds
123	Mammals
124	Scavenger (carrion)

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Aquatic bed

125	Zooplankton
126	Arthropods
127	Other invertebrates (includes mollusks)
128	Fish (eggs, fry, adults)
129	Amphibians (eggs, juveniles, adults)
130	Reptiles (eggs, juveniles, adults)
131	Birds
132	Mammals
133	Scavenger (carrion)

2.12 Feeds on animal matter within water column (i.e., on animal matter in water > 25 cm below the surface)

134	Zooplankton
135	Arthropods
136	Other invertebrates
137	Fish (eggs, fry, adults)
138	Amphibians (eggs, juveniles, adults)
139	Reptiles (eggs, juveniles, adults)
140	Birds
141	Mammals
142	Scavenger (carrion)

2.13 Feeds on animal matter at surface of water column (includes animal matter at shoreline or under shallow water [≤ 25 cm deep], in open water [≤ 25 cm deep], and on vegetation extending up to or through surface waters)

143	Zooplankton
144	Arthropods
145	Other invertebrates
146	Fish (eggs, fry, adults)
147	*Amphibians (eggs, juveniles, adults)*
148	Reptiles (eggs, juveniles, adults)
149	Birds
150	Mammals
151	Scavenger (carrion)

2.2 Feeds on animal matter in terrestrial systems

2.21 Terrestrial subsurface (to 10 cm below apparent surface)

152	Arthropods
153	Other invertebrates
154	Amphibians (juveniles, adults)
155	Reptiles (eggs, juveniles, adults)
156	Birds (eggs, nestlings, adults)
157	Mammals (nestlings, adults)
158	Scavenger (carrion)

2.22 Terrestrial surface (from 10 cm below apparent surface to 0.5 m above apparent surface)

159	Arthropods
160	Other invertebrates
161	Amphibians (juveniles, adults)
162	Reptiles (eggs, juveniles, adults)
163	Birds (eggs, nestlings, adults)
164	Mammals, small (≤ 1 kg; young, adults)
165	Mammals, large (> 1 kg; young, adults)
166	Scavenger (carrion)

2.23 Shrub strata (from 0.5 to 8.0 m above apparent surface)
- 167   Arthropods
- 168   Other invertebrates
- 169   Amphibians (juveniles, adults)
- 170   Reptiles (juveniles, adults)
- 171   Birds (eggs, nestlings, adults)
- 172   Mammals
- 173   Scavenger (carrion)

2.24 Tree boles
- 174   Arthropods
- 175   Other invertebrates
- 176   Amphibians (juveniles, adults)
- 177   Reptiles (juveniles, adults)
- 178   Birds (eggs, nestlings, adults)
- 179   Mammals
- 180   Scavenger (carrion)

2.25 Tree canopy
- 181   Arthropods
- 182   Other invertebrates
- 183   Amphibians (juveniles, adults)
- 184   Reptiles (juveniles, adults)
- 185   Birds (eggs, nestlings, adults)
- 186   Mammals
- 187   Scavenger (carrion)

2.3 Feeds on animal matter in the air above any aquatic surface or above any terrestrial strata
- 188   Arthropods
- 189   Birds
- 190   Mammals

3.0 Feeds Elsewhere
- 191   Vertebrates that breed in one or more columns (x-axis) in a habitat type but do not feed in that habitat type

Appendix II

X-coordinate Numbers (Left-hand Column) and the Corresponding Breeding Niches by Strata (Right-hand Column) used in the Determination of Wildlife Guilds

1.0 Tidal (marine and estuarine systems)

    1.1 Water typically contains a high dissolved solid (>30 ppt) content

        Bottom of water column (include substrates under water columns >25 cm deep)

001	Corral reef
002	Worm reef
003	Mollusk reef
004	Man-made structure (artificial reef)
005	Bedrock (solid rock mass)
006	Boulder (>305 mm)
007	Rubble (152–305 mm)
008	Cobble (64–152 mm)
009	Gravel (2–64 mm)
010	Sand (0.063–2 mm)
011	Mud (<0.063 mm) or organic matter (detritus or sapropel)
012	Submerged algae or moss
013	Submerged rooted vascular plants

        Water column (water >25 cm below the surface)

014	Water shallow (<2 m)
015	Water deep (>2 m)

        Surface of water column (includes substrates and vegetative cover at shoreline or under shallow water [≤25 cm deep], open water [≤25 cm deep], and types of vegetation extending up to or through surface waters)

016	Artificial (man-made) structures
017	Bedrock (solid rock mass)
018	Boulder (>305 mm)
019	Rubble (152–305 mm)
020	Cobble (64–152 mm)
021	Gravel (2–64 mm)
022	Sand (0.063–2 mm)
023	Mud (<0.063 mm) or organic matter (detritus or sapropel)
024	Aquatic bed – algae, moss, or lichen
025	Rooted herbaceous vegetation
026	Rooted woody vegetation
027	Open water
028	Floating filamentous algae (non-rooted and rooted)
029	Floating non-woody vascular plants (non-rooted)
030	Floating non-woody vascular plants (rooted)
031	Floating woody vascular plants (non-rooted)
032	Floating woody vascular plants (rooted)
033	Emergent non-woody vascular plants
034	Emergent woody vascular plants

    1.2 Water typically contains a moderate dissolved solid (0.5–30 ppt) content

        Bottom of water column (includes substrates under water columns >25 cm deep)

035	Corral reef
036	Worm reef
037	Mollusk reef
038	Man-made structure (artificial reef)
039	Bedrock (solid rock mass)

040	Boulder (>305 mm)
041	Rubble (152-305 mm)
042	Cobble (64-152 mm)
043	Gravel (2-64 mm)
044	Sand (0.063-2 mm)
045	Mud (<0.063 mm) or organic matter (detritus or sapropel)
046	Submerged algae or moss
047	Submerged rooted vascular plants

Water column (water >25 cm below the surface)

048	Water shallow (<2 m)
049	Water deep (>2 m)

Surface of water column (includes substrates and vegetative cover at shoreline or under shallow water [≤ 25 cm deep], open water [≤ 25 cm deep], and types of vegetation extending up to or through surface waters)

050	Artificial (man-made) structures
051	Bedrock (solid rock mass)
052	Boulder (>305 mm)
053	Rubble (152-305 mm)
054	Cobble (64-152 mm)
055	Gravel (2-64 mm)
056	Sand (0.063-2 mm)
057	Mud (<0.063 mm) or organic matter (detritus or sapropel)
058	Aquatic bed – algae, moss, or lichen
059	Rooted herbaceous vegetation
060	Rooted woody vegetation
061	Open water
062	Floating filamentous algae (non-rooted and rooted)
063	Floating non-woody vascular plants (non-rooted)
064	Floating non-woody vascular plants (rooted)
065	Floating woody vascular plants (non-rooted)
066	Floating woody vascular plants (rooted)
067	Emergent non-woody vascular plants
068	Emergent woody vascular plants

2.0 Non-tidal (riverine, palustrine, lacustrine systems)

2.1 Temporary waters (water usually present only at periodic intervals throughout the year)

069	Temporary wet areas (rain pools and ponds produced by irregular flooding, artificial catchments, and stock ponds temporarily filled with run-off, irrigation ditches and stream beds with seasonal flows only).

2.2 Permanent waters (water usually present throughout the year)

2.21 Species breeds in coldwater environments. Water temperature at time of breeding may typically be less than 15°C and surrounding climate is characterized with a growing season of 120-170 days with a mean July air temperature <15°C, or a growing season <120 days with a mean July air temperature <21°C.[a]

Bottom of water column (includes substrates under water columns >25 cm deep).

070	Bedrock (solid rock mass)
071	Boulder (>305 mm)
072	Rubble (152-305 mm)
073	Cobble (64-152 mm)
074	Gravel (2-64 mm)
075	Sand (0.063-2 mm)
076	Mud (<0.063 mm) or organic matter (detritus or sapropel)
077	Submerged algae or moss
078	Submerged rooted vascular plants

[a]Definition of coldwater, coolwater, and warmwater environments from McConnell, W. J., E. P. Bergersen, and K. L. Williamson (unpublished data).

Water column (water >25 cm below the surface)

079	Little or no flow (e.g., impoundments, lakes, and ponds), shallow (<2 m)
080	Little or no flow (e.g., impoundments, lakes, and ponds), deep (>2 m)
081	Laminar flow (e.g., run or smooth or slow flow in a channel), shallow (<2 m)
082	Laminar flow (e.g., run or smooth or slow flow in a channel), deep (>2 m)
083	Turbulent flow (e.g., riffle or rapid flow in a channel), shallow (<2 m)
084	Turbulent flow (e.g., riffle or rapid flow in a channel), deep (>2 m)

Surface of water column (includes substrates and vegetative cover at shoreline or under shallow water [≤25 cm deep], open water [≤25 cm deep], and types of vegetation extending up to or through surface waters)

085	Artificial (man-made) structures
086	Bedrock (solid rock mass)
087	Boulder (>305 mm)
088	Rubble (152-305 mm)
089	Cobble (64-152 mm)
090	Gravel (2-64 mm)
091	Sand (0.063-2 mm)
092	Mud (<0.063 mm) or organic matter (detritus or sapropel)
093	Aquatic bed – algae, moss, or lichen
094	Rooted herbaceous vegetation
095	Rooted woody vegetation
096	Open water
097	Floating filamentous algae (non-rooted and rooted)
098	Floating non-woody vascular plants (non-rooted)
099	Floating non-woody vascular plants (rooted)
100	Floating woody vascular plants (non-rooted)
101	Floating woody vascular plants (rooted)
102	Emergent non-woody vascular plants
103	Emergent woody vascular plants

2.22 Species breeds in coolwater environments. Water temperature at time of breeding may frequently be between 15 and 21°C but surrounding climate is characterized with a growing season >170 days with a mean July air temperature <15°C, a growing season of 120-170 days with a mean July air temperature >15°C, or a short growing season <120 days with a mean July temperature >21°C.

Bottom of water column (includes substrates under water columns >25 cm deep)

104	Bedrock (solid rock mass)
105	Boulder (>305 mm)
106	Rubble (152-305 mm)
107	Cobble (64-152 mm)
108	Gravel (2-64 mm)
109	Sand (0.063-2 mm)
110	Mud (<0.063 mm) or organic matter (detritus or sapropel)
111	Submerged algae or moss
112	Submerged rooted vascular plants

Water column (water >25 cm below the surface)

113	Little or no flow (e.g., impoundments, lakes, and ponds), shallow (<2 m)
114	Little or no flow (e.g., impoundments, lakes, and ponds), deep (>2 m)
115	Laminar flow (e.g., run or smooth or slow flow in a channel), shallow (<2 m)
116	Laminar flow (e.g., run or smooth or slow flow in a channel), deep (>2 m)
117	Turbulent flow (e.g., riffle or rapid flow in a channel), shallow (<2 m)
118	Turbulent flow (e.g., riffle or rapid flow in a channel), deep (>2 m)

Surface of water column (includes substrates and vegetative cover at shoreline or under shallow water [≤ 25 cm deep], open water [≤ 25 cm deep], and types of vegetation extending up to or through surface waters)

119	Artificial (man-made) structures
120	Bedrock (solid rock mass)
121	Boulder (> 305 mm)
122	Rubble (152–305 mm)
123	Cobble (64–152 mm)
124	Gravel (2–64 mm)
125	Sand (0.063–2 mm)
126	Mud (< 0.063 mm) or organic matter (detritus or sapropel)
127	Aquatic bed — algae, moss, or lichen
128	Rooted herbaceous vegetation
129	Rooted woody vegetation
130	Open water
131	Floating filamentous algae (non-rooted and rooted)
132	Floating non-woody vascular plants (non-rooted)
133	Floating non-woody vascular plants (rooted)
134	Floating woody vascular plants (non-rooted)
135	Floating woody vascular plants (rooted)
136	Emergent non-woody vascular plants
137	Emergent woody vascular plants

2.23 Species breeds in warmwater environments. Water temperature at time of breeding may typically be > 18°C, and surrounding climate is characterized with a growing season > 170 days with a mean July air temperature > 15°C.

Bottom of water column (includes substrates under water columns > 25 cm deep)

138	Bedrock (solid rock mass)
139	Boulder (> 305 mm)
140	Rubble (152–305 mm)
141	Cobble (64–152 mm)
142	Gravel (2–64 mm)
143	Sand (0.063–2 mm)
144	Mud (< 0.063 mm) or organic matter (detritus or sapropel)
145	Submerged algae or moss
146	Submerged rooted vascular plants

Water column (water > 25 cm below the surface)

147	Little or no flow (e.g., impoundments, lakes, and ponds), shallow (< 2 m)
148	Little or no flow (e.g., impoundments, lakes, and ponds), deep (> 2 m)
149	Laminar flow (e.g., run or smooth or slow flow in a channel), shallow (< 2 m)
150	Laminar flow (e.g., run or smooth or slow flow in a channel), deep (> 2 m)
151	Turbulent flow (e.g., riffle or rapid flow in a channel), shallow (< 2 m)
152	Turbulent flow (e.g., riffle or rapid flow in a channel), deep (> 2 m)

Surface of water column (includes substrates and vegetative cover at shoreline or under shallow water [≤ 25 cm deep], open water [≤ 25 cm deep], and types of vegetation extending up to or through surface waters)

153	Artificial (man-made) structures
154	Bedrock (solid rock mass)
155	Boulder (> 305 mm)
156	Rubble (152–305 mm)
157	Cobble (64–152 mm)
158	Gravel (2–64 mm)
159	Sand (0.063–2 mm)
160	Mud (< 0.063 mm) or organic matter (detritus or sapropel)
161	Aquatic bed — algae, moss, or lichen
162	Rooted herbaceous vegetation

163	Rooted woody vegetation
164	Open water
165	Floating filamentous algae (non-rooted and rooted)
166	Floating non-woody vascular plants (non-rooted)
167	Floating non-woody vascular plants (rooted)
168	Floating woody vascular plants (non-rooted)
169	Floating woody vascular plants (rooted)
170	Emergent non-woody vascular plants
171	Emergent woody vascular plants

3.0 Terrestrial Systems

3.1 Terrestrial subsurface (to 10 cm below apparent surface)

172	Ground burrow maker
173	Ground burrow user
174	Bank burrow maker
175	Bank burrow user
176	Cave and deep crevice
177	Artificial (man-made) structures such as mine shafts and out buildings where interior use is similar to that in burrows or caves

3.2 Terrestrial surface (from 10 cm below apparent surface to 0.5 m above apparent surface)

178	Salt playas or flats with hydric soils
179	Beaches (mud, sand, or rock) without hydrophytes
180	Marshy areas with hydrophytes but not hydric soils
181	Bare ground (sand to rubble, up to 305-mm particles)
182	Boulder (>305 mm) covered surface
183	Talus — unvegetated
184	Talus — vegetated
185	Cliff — on ledge near valley floor
186	Cliff — in cavity near valley floor
187	Cliff — on ledge near mesa or mountain top
188	Cliff — in cavity near mesa or mountain top
189	Herbaceous litter
190	Woody litter (includes shrub branches, tree branches, and stumps)
191	Grass and grasslike vegetation
192	Forb vegetation
193	Supine or dwarf woody vegetation
194	Cactus stems and pads
195	Artificial (man-made) structures — ground debris and artefacts, bridges, trestles, and rooftops where external use is analogous to that of the horizontal and vertical surface of natural objects

3.3 Shrub strata (from 0.5 to 8.0 m above apparent surface)

196	Canopy of broad-leaved deciduous shrubs
197	Canopy of needle-leaved deciduous shrubs
198	Canopy of broad-leaved evergreen shrubs
199	Canopy of needle-leaved evergreen shrubs
200	Grass and grasslike vegetation (includes bamboo) extending into shrub strata
201	Forb vegetation extending into shrub strata
202	Cactus stems and pads extending into shrub strata
203	Cavity maker — boles within shrub strata
204	Cavity user — boles within shrub strata
205	Artificial (man-made) structures — extending into shrub strata and used in a manner analogous to that of natural vegetation in the shrub strata

3.4 Tree bole

206	Snag – trunk of dead broad-leaved deciduous trees
207	Snag – trunk of dead needle-leaved deciduous trees
208	Snag – trunk of dead broad-leaved evergreen trees
209	Snag – trunk of dead needle-leaved evergreen trees
210	Cavity maker – broad-leaved deciduous trees
211	Cavity maker – needle-leaved deciduous trees
212	Cavity maker – broad-leaved evergreen trees
213	Cavity maker – needle-leaved evergreen trees
214	Cavity user – broad-leaved deciduous trees
215	Cavity user – needle-leaved deciduous trees
216	Cavity user – broad-leaved evergreen trees
217	Cavity user – needle-leaved evergreen trees
218	In or under bark – broad-leaved deciduous trees
219	In or under bark – needle-leaved deciduous trees
220	In or under bark – broad-leaved evergreen trees
221	In or under bark – needle-leaved evergreen trees
222	Snag – cactus bole or stem
223	Cavity maker – cactus bole or stem
224	Cavity user – cactus bole or stem
225	Artificial (man-made) structure – telephone and power poles. chimneys

3.5 Tree canopy

226	Small branches – live broad-leaved deciduous trees
227	Small branches – live needle-leaved deciduous trees
228	Small branches – live broad-leaved evergreen trees
229	Small branches – live needle-leaved evergreen trees
230	Large branches – live broad-leaved deciduous trees
231	Large branches – live needle-leaved deciduous trees
232	Large branches – live broad-leaved evergreen trees
233	Large branches – live needle-leaved evergreen trees
234	Large branches – dead broad-leaved deciduous trees
235	Large branches – dead needle-leaved deciduous trees
236	Large branches – dead broad-leaved evergreen trees
237	Large branches – dead needle-leaved evergreen trees

4.0 Breeds elsewhere

238	Vertebrates that feed in one or more strata during at least one season but do not breed in the habitat type

Appendix III

Vertebrate Species Breeding in Southeastern Montana and Northeastern Wyoming Used in the Species-habitat Matrices. (The species in the phenograms of Figs. 9 to 11 can be identified from these numbers.)

AMPHIBIANS

1. Tiger salamander (*Ambystoma tigrinum*)
2. Plains spadefoot toad (*Scaphiopus bombifrons*)
3. Woodhouse's toad (*Bufo woodhousei*)
4. Great plains toad (*Bufo cognatus*)
5. Dakota toad (*Bufo hemiophrys*)
6. Western chorus frog (*Pseudacris triseriata*)
7. Wood frog (*Rana sylvatica*)
8. Northern leopard frog (*Rana pipiens*)
9. Bullfrog (*Rana catesbeiana*)

REPTILES

10. Common snapping turtle (*Chelydra serpentina*)
11. Painted turtle (*Chrysemys picta*)
12. Ornate box turtle (*Terrapene ornata*)
13. Spiny softshell (*Trionyx spiniferus*)
14. Northern earless lizard (*Holbrookia maculata*)
15. Red-lipped prairie lizard (*Sceloporus undulatus*)
16. Northern sagebrush lizard (*Sceloporus graciosus*)
17. Eastern short-horned lizard (*Phrynosoma douglassi*)
18. Northern many-lined skink (*Eumeces multivirgatus*)
19. Plains hognose snake (*Heterodon nasicus*)
20. Western smooth green snake (*Opheodrys vernalis*)
21. Western yellowbelly racer (*Coluber constrictor*)
22. Bullsnake (*Pituophis melanoleucus*)
23. Central plains milk snake (*Lampropeltis triangulum*)
24. Northern redbelly snake (*Storeria occipitomaculata*)
25. Western wandering garter snake (*Thamnophis elegans*)
26. Western plains garter snake (*Thamnophis radix*)
27. Red-sided garter snake (*Thamnophis sirtalis*)
28. Prairie rattlesnake (*Crotalus viridis*)

BIRDS

29. Common loon (*Gavia immer*)
30. Red-necked grebe (*Podiceps grisegena*)
31. Horned grebe (*Podiceps auritus*)
32. Eared grebe (*Podiceps caspicus*)
33. Western grebe (*Aechmophorus occidentalis*)
34. Pied-billed grebe (*Podilymbus podiceps*)
35. Double-crested cormorant (*Phalacrocorax auritus*)
36. Great blue heron (*Ardea herodias*)
37. Black-crowned night heron (*Nycticorax nycticorax*)
38. American bittern (*Botaurus lentiginosus*)
39. Canada goose (*Branta canadensis*)
40. Mallard (*Anas platyrhynchos*)
41. Gadwall (*Anas strepera*)
42. Pintail (*Anas acuta*)
43. Blue-winged teal (*Anas discors*)
44. Green-winged teal (*Anas crecca*)
45. American wigeon (*Anas americana*)
46. Northern shoveler (*Anas clypeata*)
47. Redhead (*Aythya americana*)
48. Canvasback (*Aythya valisineria*)
49. Lesser scaup (*Aythya affinis*)
50. Harlequin duck (*Histrionicus histrionicus*)
51. Ruddy duck (*Oxyura jamaicensis*)
52. Hooded merganser (*Lophodytes cucullatus*)
53. Common merganser (*Mergus merganser*)
54. Turkey vulture (*Cathartes aura*)
55. Goshawk (*Accipiter gentilis*)
56. Sharp-shinned hawk (*Accipiter striatus*)
57. Cooper's hawk (*Accipiter cooperii*)
58. Red-tailed hawk (*Buteo jamaicensis*)
59. Swainson's hawk (*Buteo swainsoni*)
60. Ferruginous hawk (*Buteo regalis*)
61. Golden eagle (*Aquila chrysaetos*)
62. Marsh hawk (*Circus cyaneus*)
63. Osprey (*Pandion haliaetus*)
64. Prairie falcon (*Falco mexicanus*)
65. American kestrel (*Falco sparverius*)
66. Ruffed grouse (*Bonasa umbellus*)
67. Blue grouse (*Dendragapus obscurus*)
68. Sharp-tailed grouse (*Pedioecetes phasianellus*)
69. Sage grouse (*Centrocercus urophasianus*)
70. Ring-necked pheasant (*Phasianus colchicus*)
71. Gray partridge (*Perdix perdix*)
72. Merriam's turkey (*Meleagris gallopavo*)
73. Sandhill crane (*Grus canadensis*)
74. Virginia rail (*Rallus limicola*)
75. Sora (*Porzana carolina*)
76. American coot (*Fulica americana*)
77. Piping plover (*Charadrius melodus*)
78. Killdeer (*Charadrius vociferus*)
79. Mountain plover (*Eupoda montana*)
80. Common snipe (*Capella gallinago*)
81. Long-billed curlew (*Numenius americanus*)
82. Upland sandpiper (*Bartramia longicauda*)
83. Spotted sandpiper (*Actitis macularia*)
84. Willet (*Catoptrophorus semipalmatus*)
85. Marbled godwit (*Limosa fedoa*)
86. American avocet (*Recurvirostra americana*)
87. Wilson's phalarope (*Steganopus tricolor*)
88. Ring-billed gull (*Larus delawarensis*)
89. Common tern (*Sterna hirundo*)
90. Black tern (*Chlidonias niger*)
91. Rock dove (*Columba livia*)
92. Mourning dove (*Zenaida macroura*)
93. Yellow-billed cuckoo (*Coccyzus americanus*)
94. Black-billed cuckoo (*Coccyzus erythropthalmus*)

95. Screech owl (*Otus asio*)
96. Great horned owl (*Bubo virginianus*)
97. Pygmy owl (*Glaucidium gnoma*)
98. Burrowing owl (*Athene cunicularia*)
99. Long-eared owl (*Asio otus*)
100. Short-eared owl (*Asio flammeus*)
101. Saw-whet owl (*Aegolius acadicus*)
102. Poor-Will (*Phalaenoptilus nuttallii*)
103. Common nighthawk (*Chordeiles minor*)
104. Chimney swift (*Chaetura pelagica*)
105. White-throated swift (*Aeronautes saxatalis*)
106. Belted kingfisher (*Megaceryle alcyon*)
107. Common flicker (*Colaptes auratus*)
108. Red-headed woodpecker (*Melanerpes erythrocephalus*)
109. Lewis' woodpecker (*Melanerpes lewis*)
110. Yellow-bellied sapsucker (*Sphyrapicus varius*)
111. Williamson's sapsucker (*Sphyrapicus thyroideus*)
112. Hairy woodpecker (*Picoides villosus*)
113. Downy woodpecker (*Picoides pubescens*)
114. Black-backed three-toed woodpecker (*Picoides arcticus*)
115. Eastern kingbird (*Tyrannus tyrannus*)
116. Western kingbird (*Tyrannus verticalis*)
117. Say's phoebe (*Sayornis saya*)
118. Willow flycatcher (*Empidonax traillii*)
119. Least flycatcher (*Empidonax minimus*)
120. Dusky flycatcher (*Empidonax oberholseri*)
121. Western flycatcher (*Empidonax difficilis*)
122. Hammond's flycatcher (*Empidonax hammondii*)
123. Western wood pewee (*Contopus sordidulus*)
124. Horned lark (*Eremophila alpestris*)
125. Violet-green swallow (*Tachycineta thalassina*)
126. Tree swallow (*Iridoprocne bicolor*)
127. Bank swallow (*Riparia riparia*)
128. Rough-winged swallow (*Stelgidopteryx ruficollis*)
129. Barn swallow (*Hirundo rustica*)
130. Cliff swallow (*Petrochelidon pyrrhonota*)
131. Gray jay (*Perisoreus canadensis*)
132. Steller's jay (*Cyanocitta stelleri*)
133. Black-billed magpie (*Pica pica*)
134. Common raven (*Corvus corax*)
135. Common crow (*Corvus brachyrhynchos*)
136. Pinyon jay (*Gymnorhinus cyanocephalus*)
137. Clark's nutcracker (*Nucifraga columbiana*)
138. Black-capped chickadee (*Parus atricapillus*)
139. Mountain chickadee (*Parus gambeli*)
140. White-breasted nuthatch (*Sitta carolinensis*)
141. Red-breasted nuthatch (*Sitta canadensis*)
142. Brown creeper (*Certhia familiaris*)
143. Dipper (*Cinclus mexicanus*)
144. House wren (*Troglodytes aedon*)
145. Long-billed marsh wren (*Cistothorus palustris*)
146. Canyon wren (*Catherpes mexicanus*)
147. Rock wren (*Salpinctes obsoletus*)
148. Gray catbird (*Dumetella carolinensis*)
149. Brown thrasher (*Toxostoma rufum*)
150. Sage thrasher (*Oreoscoptes montanus*)
151. American robin (*Turdus migratorius*)
152. Hermit thrush (*Catharus guttatus*)
153. Swainson's thrush (*Catharus ustulatus*)
154. Veery (*Catharus fuscescens*)
155. Eastern bluebird (*Sialia sialis*)
156. Mountain bluebird (*Sialia currucoides*)
157. Townsend's solitaire (*Myadestes townsendi*)
158. Golden-crowned kinglet (*Regulus satrapa*)
159. Ruby-crowned kinglet (*Regulus calendula*)
160. Sprague's pipit (*Anthus spragueii*)
161. Cedar waxwing (*Bombycilla cedrorum*)
162. Loggerhead shrike (*Lanius ludovicianus*)
163. Starling (*Sturnus vulgaris*)
164. Solitary vireo (*Vireo solitarius*)
165. Red-eyed vireo (*Vireo olivaceus*)
166. Warbling vireo (*Vireo gilvus*)
167. Orange-crowned warbler (*Vermivora celata*)
168. Yellow warbler (*Dendroica petechia*)
169. Ovenbird (*Seiurus aurocapillus*)
170. Common yellowthroat (*Geothlypis trichas*)
171. Yellow-breasted chat (*Icteria virens*)
172. Wilson's warbler (*Wilsonia pusilla*)
173. American redstart (*Setophaga ruticilla*)
174. House sparrow (*Passer domesticus*)
175. Bobolink (*Dolichonyx oryzivorus*)
176. Western meadowlark (*Sturnella neglecta*)
177. Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)
178. Red-winged blackbird (*Agelaius phoeniceus*)
179. Orchard oriole (*Icterus spurius*)
180. Northern oriole (*Icterus galbula*)
181. Brewer's blackbird (*Euphagus cyanocephalus*)
182. Common grackle (*Quiscalus quiscula*)
183. Brown-headed cowbird (*Molothrus ater*)
184. Western tanager (*Piranga ludoviciana*)
185. Black-headed grosbeak (*Pheucticus melanocephalus*)
186. Lazuli bunting (*Passerina amoena*)
187. Dickcissel (*Spiza americana*)
188. Evening grosbeak (*Hesperiphona vespertina*)
189. Cassin's finch (*Carpodacus cassinii*)
190. House finch (*Carpodacus mexicanus*)
191. Pine grosbeak (*Pinicola enucleator*)
192. Gray-crowned rosy finch (*Leucosticte tephrocotis*)
193. Black rosy finch (*Leucosticte atrata*)
194. Pine siskin (*Carduelis pinus*)
195. American goldfinch (*Carduelis tristis*)
196. Red crossbill (*Loxia curvirostra*)
197. Green-tailed towhee (*Pipilo chlorurus*)
198. Rufous-sided towhee (*Pipilo erythrophthalmus*)
199. Lark bunting (*Calamospiza melanocorys*)
200. Savannah sparrow (*Passerculus sandwichensis*)
201. Grasshopper sparrow (*Ammodramus savannarum*)
202. Baird's sparrow (*Ammodramus bairdii*)
203. Vesper sparrow (*Pooecetes gramineus*)
204. Lark sparrow (*Chondestes grammacus*)
205. Dark-eyed junco (*Junco hyemalis*)

206. Chipping sparrow (*Spizella passerina*)
207. Clay-colored sparrow (*Spizella pallida*)
208. Brewer's sparrow (*Spizella breweri*)
209. White-crowned sparrow (*Zonotrichia leucophrys*)
210. Lincoln's sparrow (*Melospiza lincolnii*)
211. Song sparrow (*Melospiza melodia*)
212. McCown's longspur (*Rhynchophanes mccownii*)
213. Chestnut-collared longspur (*Calcarius ornatus*)

MAMMALS

214. Masked shrew (*Sorex cinereus*)
215. Merriam's shrew (*Sorex merriami*)
216. Little brown myotis (*Myotis lucifugus*)
217. Yuma myotis (*Myotis yumanensis*)
218. Long-eared myotis (*Myotis evotis*)
219. Long-legged myotis (*Myotis volans*)
220. Small-footed myotis (*Myotis leibii*)
221. Silver-haired bat (*Lasionycteris noctivagans*)
222. Big brown bat (*Eptesicus fuscus*)
223. Hoary bat (*Lasiurus cinereus*)
224. Townsend's big-eared bat (*Plecotus townsendii*)
225. Eastern cottontail (*Sylvilagus floridanus*)
226. Nuttall's cottontail (*Sylvilagus nuttallii*)
227. Desert cottontail (*Sylvilagus audubonii*)
228. White-tailed jackrabbit (*Lepus townsendii*)
229. Black-tailed jackrabbit (*Lepus californicus*)
230. Least chipmunk (*Eutamias minimus*)
231. Yellow-bellied marmot (*Marmota flaviventris*)
232. Richardson's ground squirrel (*Spermophilus richardsonii*)
233. Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)
234. Spotted ground squirrel (*Spermophilus spilosoma*)
235. Black-tailed prairie dog (*Cynomys ludovicianus*)
236. White-tailed prairie dog (*Cynomys leucurus*)
237. Fox squirrel (*Sciurus niger*)
238. Red squirrel (*Tamiasciurus hudsonicus*)

239. Northern pocket gopher (*Thomomys talpoides*)
240. Plains pocket gopher (*Geomys bursarius*)
241. Olive-backed pocket mouse (*Perognathus fasciatus*)
242. Plains pocket mouse (*Perognathus flavescens*)
243. Silky pocket mouse (*Perognathus flavus*)
244. Hispid pocket mouse (*Perognathus hispidus*)
245. Ord's kangaroo rat (*Dipodomys ordii*)
246. Beaver (*Castor canadensis*)
247. Western harvest mouse (*Reithrodontomys megalotis*)
248. Deer mouse (*Peromyscus maniculatus*)
249. White-footed mouse (*Peromyscus leucopus*)
250. Northern grasshopper mouse (*Onychomys leucogaster*)
251. Bushy-tailed wood rat (*Neotoma cinerea*)
252. Meadow vole (*Microtus pennsylvanicus*)
253. Long-tailed vole (*Microtus longicaudus*)
254. Prairie vole (*Microtus ochrogaster*)
255. Sagebrush vole (*Lagurus curtatus*)
256. Muskrat (*Ondatra zibethicus*)
257. House mouse (*Mus musculus*)
258. Meadow jumping mouse (*Zapus hudsonius*)
259. Porcupine (*Erethizon dorsatum*)
260. Coyote (*Canis latrans*)
261. Red fox (*Vulpes vulpes*)
262. Swift fox (*Vulpes velox*)
263. Black bear (*Ursus americanus*)
264. Raccoon (*Procyon lotor*)
265. Long-tailed weasel (*Mustela frenata*)
266. Mink (*Mustela vison*)
267. Badger (*Taxidea taxus*)
268. Western spotted skunk (*Spilogale gracilis*)
269. Striped skunk (*Mephitis mephitis*)
270. Lynx (*Felis lynx*)
271. Bobcat (*Felis rufus*)
272. Elk (*Cervus elaphus*)
273. Mule deer (*Odocoileus hemionus*)
274. White-tailed deer (*Odocoileus virginianus*)
275. Pronghorn (*Antilocapra americana*)

A list of current *Special Scientific Report – Wildlife* follows.

225. Scalation of the American Alligator, by Charles A. Ross and Charles D. Roberts. 1979. 8 pp.

(Reports 226 and 227 are in one cover)
226. Waterfowl Status Report, 1975, compiled and edited by James R. Goldsberry, Sharon L. Rhoades, Lonnie D. Schroeder, and Morton M. Smith. 1980. 86 pp.
227. Waterfowl Status Report, 1976, compiled and edited by William W. Larned, Sharon L. Rhoades, and K. Duane Norman. 1980. 88 pp.
228. Effects of Environmental Contaminants on Reptiles: A Review, by Russell J. Hall. 1980. 12 pp.
229. The Rocky Mountain Population of the Western Canada Goose: Its Distribution, Habitats, and Management, by William B. Krohn and Elwood G. Bizeau. 1980. 93 pp.
230. Breeding Biology and Relation of Pollutants to Black Skimmers and Gull-billed Terns in South Carolina, by Lawrence J. Blus and Charles J. Stafford. 1980. 18 pp.
231. The Canada Goose (*Branta canadensis*) – An Annotated Bibliography, compiled by Scott R. Craven. 1981. 66 pp.
232. Metabolism of Pesticides: Update III, by Calvin M. Menzie. 1980. 709 pp.
233. Relative Attractiveness of Different Foods at Wild Bird Feeders, by Aelred D. Geis. 1980. 11 pp.
234. Establishment of Seeded Grasslands for Wildlife Habitat in the Prairie Pothole Region, by Harold F. Duebbert, Erling T. Jacobson, Kenneth E. Higgins, and Erling B. Podoll. 1981. 21 pp.
235. Bats and Environmental Contaminants: A Review, by Donald R. Clark, Jr. 1981. 27 pp.

(Reports 236 and 237 are in one cover)
236. Waterfowl Status Report, 1977, compiled and edited by Carey S. Smith, Sharon L. Rhoades, and K. Duane Norman. 1981. 88 pp.
237. Waterfowl Status Report, 1978, compiled and edited by Albert N. Novara, Sharon L. Rhoades, Betty I. Hodges, and K. Duane Norman. 1981. 96 pp.
238. Status Reports on Twelve Raptors, by David L. Evans. 1982. 68 pp.
239. Summary of Foreign Game Bird Liberations, 1969–78, by Richard C. Banks. 1981. 23 pp.
240. Reliability of Kill and Activity Estimates in the U.S. Waterfowl Hunter Survey, by Leigh M. Couling, A. R. Sen, and Elwood M. Martin. 1982. 14 pp.
241. Residues of DDT, Dieldrin, and Heptachlor in Earthworms During Two Years Following Application, by Charles D. Gish and Donald L. Hughes. 1982. 15 pp.
242. Changes in Vegetation Structure in Seeded Nesting Cover in the Prairie Pothole Region, by Kenneth F. Higgins and William T. Barker. 1982. 25 pp.
243. Bibliography of References to Avian Botulism: Update, by Sonoma S. Wilson and Louis N. Locke. 1982. 10 pp.

Application of the Guild Concept to Environmental Impact Analysis of Terrestrial Vegetation

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The necessity for environmental impact assessments (EIA) and environmental impact statements (EIS) has become widespread since the passage of the National Environmental Policy Act of 1969 (NEPA), though the unstandardized methodology for data collection and interpretation allows different decisions and recommendations to be reached by different personnel. Ideally, more standardized and rigorous procedures would lead to a more objective evaluation of an area's ecological value.

Here, the application of the guild concept for classifying terrestrial vegetation is presented and discussed. A dichotomous key of ecological characteristics valuable for examining succession and environmental impact is provided. These characteristics were also chosen to provide clear-cut placement of plant species into a specific guild, thus eliminating much of the subjectivity of classification. The characteristics included are growth form (woody v. herbaceous), leaf persistence (evergreen v. deciduous), ability to fix nitrogen, principal mode of dispersal, type of breeding-pollination system, and life form (annual v. perennial). The guild characteristics are examined and predictions are made regarding the relative order of guild appearance during post-disturbance recolonization. By comparing pre- and post-disturbance guild inventories, the extent of degradation can be determined and particularly sensitive guilds can be examined. Overall, it is hoped that this classification scheme will better reveal the extent of damage, speed of recovery, and predictive accuracy of the EIA/EIS.

Keywords: environmental impact analysis, guilds, plants, leaf persistence, growth form, nitrogen fixing ability, mode of dispersal, breeding-pollination system, life form.

1. Introduction

The National Environmental Policy Act of 1969 (NEPA) set forth requirements aimed to improve the basis for making decisions regarding "Federal actions significantly affecting the quality of the human environment". To determine a project's potential impact upon an area better, environmental impact assessments (EIA) and environmental

impact statements (EIS) became necessary, requiring an interdisciplinary team of personnel and the expenditure of large sums of money.

An ecologist must survey large, diverse natural communities supporting up to several thousand species and predict potential impact after extremely short periods of fieldwork. Hence, ecologists often collect only species composition data indicating at best the relative abundances of different species, i.e. abundant, common, rare, or absent. An exception is for threatened or endangered species, this being largely due to the more stringent requirements of the Endangered Species Act of 1973. Regardless, many data are left unanalyzed and at best incorporated in the appendices of an EIA/EIS. Consequently, the EIA/EIS may become a rather imprecise description of an area's ecological components; as a result, different interpretations may be arrived at by different reviewers.

Ideally, a more standard procedure would lead to more objective judgements and allow comparisons of natural areas by their relative ecological value. By favoring standardization, NEPA has created a better decision-making process and encouraged ecologists to develop methods of comparing and interpreting complex organized communities more rigorously. Using the guild concept, I propose a more concise approach to determine impact on terrestrial vegetation.

Root (1967) defined an ecological guild as "a group of species that exploit the same class of environmental resources in a similar way". Each guild consists of species possessing common ecological characteristics, regardless of taxonomic affinity. Subsequently, the concept has been applied to community structure of collards and their susceptibility to herbivorous arthropods (Root, 1973), resource partitioning in some parasitic insects (Price, 1971), foraging preferences in avian species (Karr, 1971; Willson, 1974), fugitive plant species (Platt, 1975), and reproductive groups of fishes based on preferred spawning grounds and reproductive behavior (Balon, 1975a, b).

The objectives of this paper are to describe and rationalize characteristics used to delineate guilds of terrestrial vegetation. The classification's potential usefulness in accurately assessing damage and for predicting an area's speed of recovery is then illustrated. Lastly, a methodology to interpret quantitatively the extent of disturbance, time for recovery, and changes in community structure and function is proposed.

2. The proposed classification system

I have divided terrestrial vegetation into ninety-five guilds based on growth and life form, nitrogen-fixing ability, leaf persistence, and breeding system or pollination vector (Figure 1). The logic of this classification is based primarily on the relative ability of the species to disperse, become established, and propagate at a new site (see Diamond, 1975, for a discussion on community assembly). By emphasizing dispersal, this system should be useful in predicting recolonization time. The degree of degradation of a disturbed site can be assessed by using representative species of a guild as indicators in the successional process.

In developing the proposed system, a restricted number of ecological characteristics of a species were chosen that are objective, and yet have value for environmental impact considerations. Consequently, several physiological factors important for establishment, such as root structure, seed dormancy, asexual reproduction, and tolerance to moisture, nutrients, and light were discarded because individuals may respond differently in different habitats or soils. Much of the uncertainty of classification is therefore eliminated with species fitting into only one guild.

The breakdowns into biotic and abiotic factors represent arbitrary divisions that provide a dichotomous dendrogram for placement of plant species. The system first

Abiotic pollination — Autogamous — *Picea abies*

Wind and water

Abiotic pollination — Wind — *Pinus echinata*

Biotic pollination — Insect

Abiotic dispersal

Gravity

Abiotic pollination — Autogamous

Abiotic pollination — Wind

Biotic pollination — Insect — *Kalmia latifolia, K. polifolia, Chamaedaphne calyculata*

No N₂ fixation

Bird

Abiotic pollination — Autogamous

Abiotic pollination — Wind — *Juniperus californica, J. virginiana*

Biotic pollination — Insect — *Yucca elata, Y. brevifolia, Ilex opaca, Empetrum nigrum*

Biotic dispersal

Mammal

Abiotic pollination — Autogamous

Abiotic pollination — Wind — *Andromeda glaucophylla, Carica papaya, Pinus monticola, Pseudotsuga menziesii*

Biotic pollination — Insect

Woody-evergreen

Wind and water

Abiotic pollination — Autogamous

Abiotic pollination — Wind

Biotic pollination — Insect

Abiotic dispersal

Gravity

Abiotic pollination — Autogamous

Abiotic pollination — Wind

Biotic pollination — Insect

N₂ fixation

Bird

Abiotic pollination — Autogamous

Abiotic pollination — Wind

Biotic pollination — Insect — *Myrica inodora, M. cerifera, M. pennsylvanica, M. heterophylla*

Biotic dispersal

Mammal

Abiotic pollination — Autogamous

Abiotic pollination — Wind

Biotic pollination — Insect

Figure 1, Part 1. Guilds of terrestrial vegetation inhabiting the United States

Figure 1, Part 2. Guilds of terrestrial vegetation inhabiting the United States.
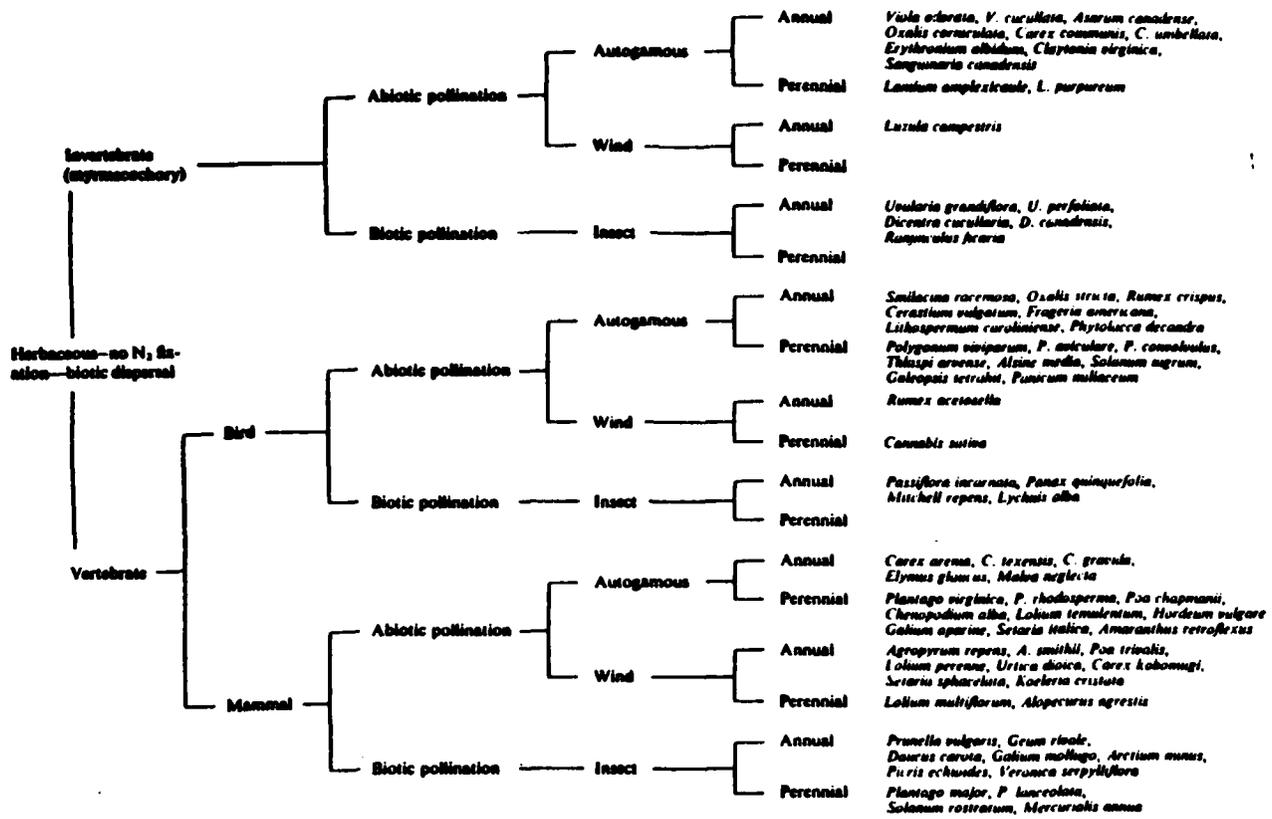
Figure 1, Part 3. Guilds of terrestrial vegetation inhabiting the United States.
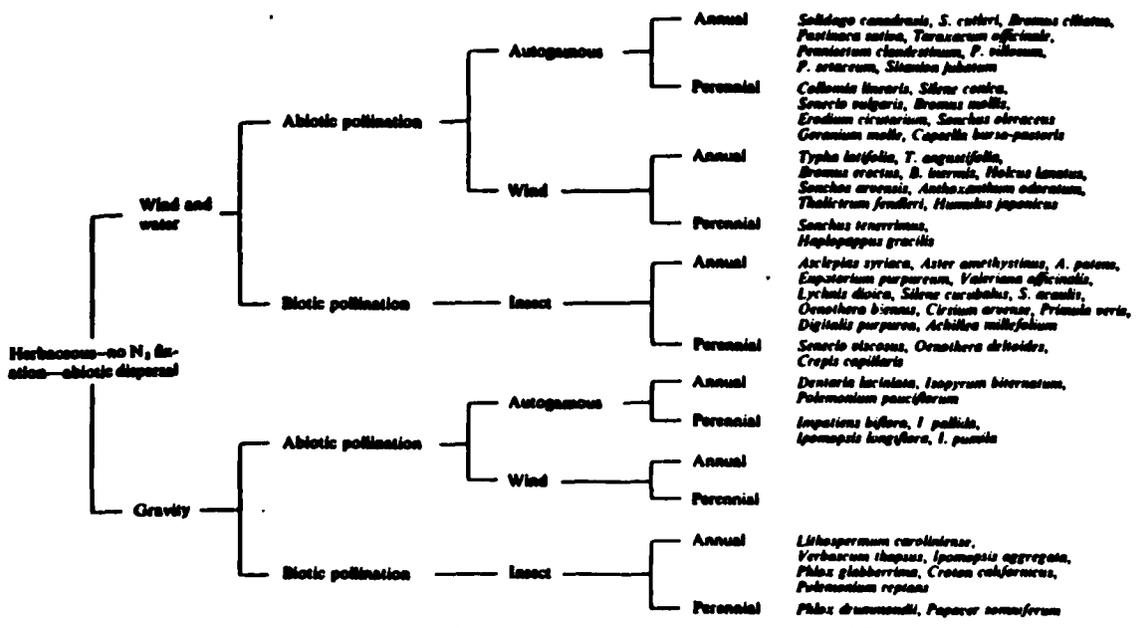
Figure 1, Part 4. Guilds of terrestrial vegetation inhabiting the United States.
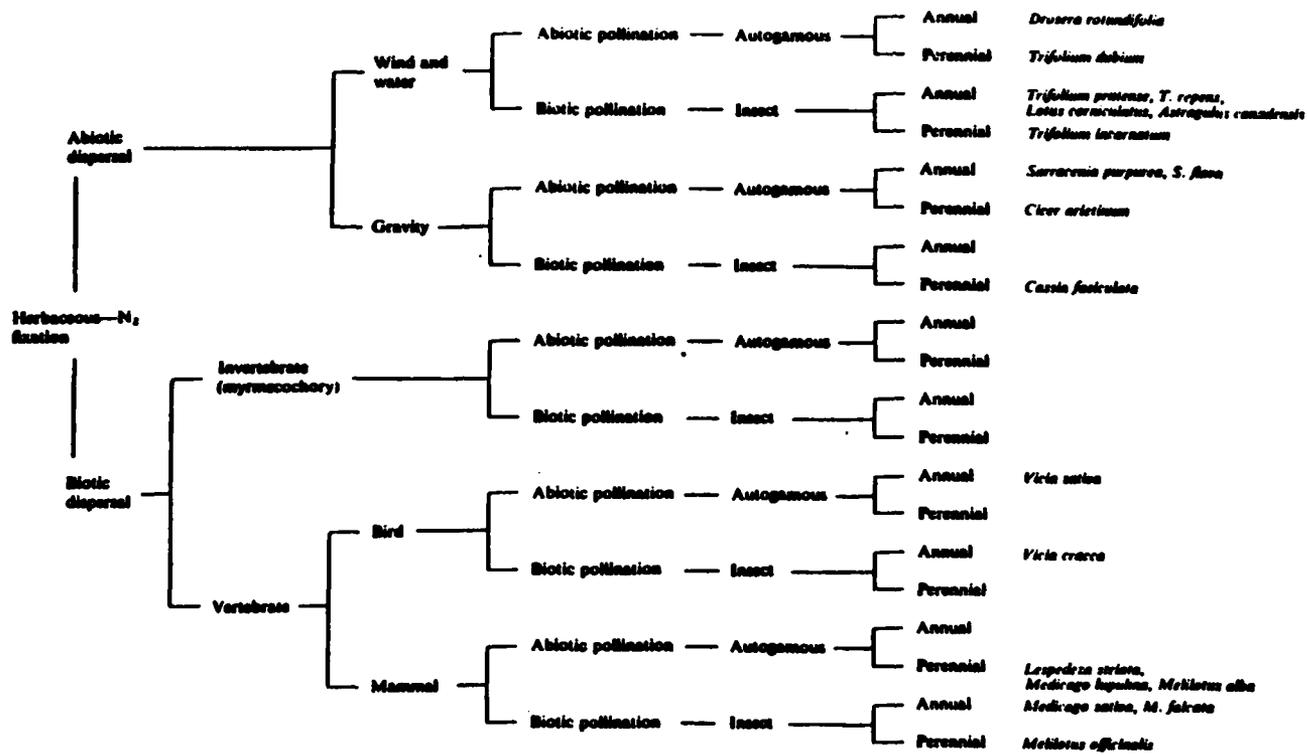
Figure 1, Part 5. Guilds of terrestrial vegetation inhabiting the United States.

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divides species based on competitive ability and adaptations for establishment. These include the woody v. herbaceous, leaf persistence, and nitrogen-fixing ability categories. Dispersal is considered next as it ultimately determines which species arrive at a site. Lastly, the breeding-pollination system and life form classification are used as indicators of ability to reproduce, disseminate, and become successful in the surrounding area.

The species are first divided into woody and herbaceous plants. Apart from the gross morphological differences, the woody habit gives the advantage of combining perenniality and height. Consequently, neighbours may be shaded, flowers may be more accessible to pollinators or to the wind, and seeds may be shed over greater distances (Harper, 1977). Seeds of some woody species may colonize an area at rates similar to herbaceous species, though their reproductive contribution to the community is delayed several years until maturity. The time required to attain structural development of the woody stratum constitutes a bottleneck to later successional woody guilds depending on active transport by mammals that typically avoid areas of insufficient tree development. Consequently, species of the equivalent herbaceous guild may progress through the successional sequence more rapidly than woody guilds.

Leaf persistence (deciduous or evergreen) is another relevant growth-form characteristic of woody plants. One form is typically dominant in a given climatic region (Mooney, 1974), with the relative advantages in particular climates being due to differences in drought tolerance, nutrient retention, and length of growing season (Axelrod, 1966; Monk, 1966; Mooney, 1974; Harper, 1977; Miller, 1979). I attempted to use clear-cut examples in the system, though a few species are tardily deciduous and were placed in the evergreen category (U.S. Forest Service, 1948; Brockman, 1968).

The ability to fix nitrogen is critical where vegetation has been disturbed or removed. Nutrient losses due to leaching and erosion increase dramatically following disturbance, nitrogen being depleted in the largest quantities (Bormann et al., 1969; Marks and Bormann, 1972; Likens and Bormann, 1972). Plants capable of escaping the need for soil nitrogen on disturbed sites or areas low in available nitrogen are at a competitive advantage and are often pioneer species on these soils (Stewart, 1967; Harper, 1977). Consequently, nitrogen fixers often do well on early successional sites, such as strip-mined areas, where available nitrogen is low. These plants enhance conditions for other invading plants requiring soil nitrogen. Nitrogen-fixing plants include many species of the family Leguminosae, several non-leguminous species (Stewart, 1967), and insectivorous plants (Schnell, 1976) (nitrogen-fixing ability is used to mean a lack of dependence on soil nitrogen).

Species differ in their ease and modes of dispersal. The relative effectiveness of each has implications for the relative order of arrival at a site. Generally, animal dispersal is much more effective over long distances, such as to oceanic islands, and is adaptive in a wider range of habitats (Stebbins, 1971). Wind-dispersed species are often quickest to invade and establish on disturbed sites, since the sites may be surrounded by potential colonizers. This trend is supported by data from recently strip-mined areas bearing such wind-dispersed species as *Solidago* spp., *Typha latifolia*, *Pastinaca sativa*, *Populus deltoides*, *Platanus occidentalis*, *Fraxinus* spp., and *Campsis radicans* (Wetzel, 1958; Karr, 1968).

Animal-dispersed species usually arrive at a disturbed site after wind-dispersed species because animals move preferentially into habitats having a characteristic vegetational structure and avoid travel over extremely different habitats (Baker, 1966; Stebbins, 1971). Seeds dispersed by mammals, whether it be externally or internally, may lack the ability to colonize disturbed sites promptly until some revegetation occurs. Small

mammals such as the deer mouse (*Peromyscus maniculatus*) may begin to repopulate previously disturbed areas after about five years and provide dispersal via caching for species such as *Lespedeza* spp. (Howard, 1949). Most other early successional small mammals are not seed-eaters (see Severinghaus and Balbach, 1979, for seed-eating mammals) and provide dispersal only by epizoochory (external adhesion) (Wetzel, 1958). Areas strip-mined 25 years previously had not yet been invaded by the squirrel *Sciurus niger* from nearby forested areas because of insufficient tree development (Wetzel, 1958).

Alternatively, bird-dispersed species may colonize quickly over long distances through extended retention of seeds in the digestive tract (Proctor, 1968) and long migrations. Short distance dispersal occurs by regurgitating seeds of recently eaten fruits (McKey, 1975). Thus, bird-dispersed species often colonize more quickly than mammalian-dispersed species.

Dispersal by gravity includes species whose seeds have no obvious means of transport or are released ballistically. Consequently, the distance of transport is usually limited to several meters from the parent (Stebbins, 1971).

Myrmecochory, or seed dispersal by ants, is also deemed an important method of dispersal, particularly for herbs living in dense forests (Stebbins, 1971). Transport distance is relatively small and probably only slightly more than ballistically dispersed species, though myrmecochorous species enjoy the advantage of seed placement in a suitable site (van der Pijl, 1969; Culver and Beattie, 1978). Thus, the dispersal is precise and the probability of germination and establishment is enhanced.

Overall, I expect that wind-dispersed species will arrive most rapidly at a disturbed site, followed in turn by bird, mammal, ant, and finally gravity or ballistically-dispersed species.

I classified plant species by their primary mode of dispersal (for dispersal in general see Ridley, 1930; Stebbins, 1971, 1974; van der Pijl, 1969; Wood, 1974; Harper, 1977; for myrmecochory Berg, 1966; Handel, 1978; Schemske *et al.*, 1978; Culver and Beattie, 1978; for birds and mammals McAtee, 1947; Krefting and Roe, 1949; Martin, Zim and Nelson, 1951; Smith, 1975; Thompson and Willson, 1978). Species having polymorphic seeds, i.e. some members of Compositae, Leguminosae, and Cruciferae (Stebbins, 1971), some being adapted for wind or animal transport and others displaying no obvious means of dispersal, were placed in the guild having the highest dispersal potential.

A species breeding-pollination system is important in determining whether the individuals reproduce and spread in an area after arriving. Three types of breeding-pollination systems were distinguished: autogamous (self-compatible) plants, that may or may not require the aid of a pollinating vector to produce seeds (Proctor and Yeo, 1972), allogamous (self-incompatible) and dioecious wind-pollinated plants, and allogamous and dioecious insect-pollinated plants (for autogamous and allogamous species, see Fryxell, 1957; Whitehouse, 1959; Grant and Grant, 1965; Mulligan and Findlay, 1970; Mulligan, 1972; Wood, 1974; Gibbs, Milne and Carillo, 1975; de Nettancourt, 1977; Frankel and Galun, 1977; for allogamy, East, 1929, 1940; Reader, 1975; for autogamy, Uphof, 1938; Schemske *et al.*, 1978; for dioecy, Yampolsky and Yampolsky, 1922; Allen, 1940; Mather, 1940; Grant, 1975; for pollination by wind or insects, Faegri and van der Pijl, 1966; Proctor and Yeo, 1972; Stebbins, 1974; Wood, 1974; de Nettancourt, 1977).

These three systems represent a breakdown that implies a hierarchial ability to reproduce successfully on disturbed areas once establishment has occurred. Autogamy is generally regarded as an adaptive strategy for plants occupying temporary pioneer habitats (Allard, 1965; Stebbins, 1970; Frankel and Galun, 1977) because long-distance

dispersal of a single propagule can lead to rapid population increases. This system is also adaptive for colonizing species because of the possible lack of predictable pollinator services (Levin, 1972). Autogamy is commonly found in annuals, while perennial species in the same or a closely related genus are often obligate outcrossers (Stebbins, 1974). Consequently, autogamous species are expected to do better than allogamous species on recently disturbed sites.

Allogamous and dioecious species, because they both need pollen from a separate plant, may be spatially isolated, and thus fail to reproduce on a heavily disturbed site. This category is divided into plants pollinated by wind and by insects, as each vector is advantageous in different conditions. Wind-pollinated flowers, which are taxonomically restricted (Faegri and van der Pijl, 1966; Stebbins, 1974), are independent of the possibly erratic and inconstant behavior of insects (Ridley, 1930; Proctor and Yeo, 1972). Optimum conditions for wind pollination are found in open, sparse vegetation or in the top layer of closed, multi-layered vegetation types (Faegri and van der Pijl, 1966). Wind-pollinated species should be reproductively successful before insect-pollinated species as insects tend to be preferentially attracted to larger densities of flowers (Platt, Hill and Clark, 1974) which may be lacking immediately after a disturbance has occurred. Vertebrate pollination was not included as a distinct class as many of the vertebrate-pollinated species (about 150 in the United States) (James, 1948; Grant and Grant, 1968; Austin, 1975) are either autogamous (Grant and Grant, 1965, 1968) or are also successfully pollinated by insects (Grant and Grant, 1968).

Lastly, the herbaceous species are divided into annual and biennials/perennials (Munz, 1968; Fernald, 1970; Britton and Brown, 1970). Perennials such as *Festuca ovina* may form long-lived genets (Cook, 1979) that need to reproduce successfully sexually in occasional years for further colonization of the site. Annuals must produce seeds every year if reproduction and colonization of the site is to continue. Non-autogamous annuals may have a short-lived existence at a site if sufficient pollen does not reach the flowers.

3. Applications

The guild concept has potential use in environmental impact analysis though it has only recently been introduced for mammals (Severinghaus and Balbach, unpublished). By assembling species into functionally similar groups based on ecology and life history requirements, one may be able to predict the impact upon the components of a community for a given project and devise methods to mitigate the impact where desired. The system should be useful in predicting recolonization time or assessing the degree of degradation of a disturbed site. Each requires a survey prior to and after the disturbance to assemble a guild inventory for both the area to be disturbed and the surrounding area (this representing potential recolonizing species).

An area's guilds are delineated by plot sampling using rectangular plots with sides in a ratio of 1 : 2. For closely-spaced herbaceous vegetation, use plots 1 m² in area on a scale of 1 : 2 (i.e. 0·71 × 1·41 m). For bushes, shrubs, and saplings up to 3 to 4 m tall, use 10 m² plots (2·24 × 4·47 m). For forest trees over 3 to 4 m tall, use 100 m² plot (7·07 × 14·14 m) sampling areas. The number of plots needed for a reliable estimate of the guild inventory is determined by using species-area and performance curves (Brower and Zar, 1977). This technique also determines the relative abundance of each guild, such that similarity indices can be used to quantify the differences of two communities or one community at different times (Huhta, 1979). The guild inventory itself gives an overview of the general community structure and stage of succession.

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The extent of damage is assessed by comparing the pre- and post-disturbance guild inventory. All guilds are classified at each division of the scheme, *i.e.* nitrogen-fixing ability, principal mode of dispersal, etc. Each class is weighted by the expected order of arrival, this representing a relative replacement time. The magnitude of disturbance is estimated by comparing the proportionate losses among the classes of each division. As

TABLE 1. Estimated replacement time for gross habitats in Illinois. Taken from Graber and Graber (1976)

Gross habitats	Years of successional lead-in time	Years of replacement time	References
Bottomland forest			
Oak–gum–cypress	100–150	20–600	Anderson and White (1970), Shelford (1954)
Elm–ash–cottonwood by age			
5–29 years	35	5–29	Shelford (1954)
(willow–cottonwood)			
30–59 years	35	30–59	Shelford (1954)
(willow–cottonwood–maple)			
60–99 years	35	60–99	Shelford (1954)
(hackberry–gum)			
100+	135–600	100–500†	Shelford (1954)
(hackberry–gum, elm–oak–hickory, and succession to climax)			
Upland forest by age			
10–29 years	25	10–29	Bazzaz (1968), Beckwith (1954)
(black cherry–elm–hawthorn, elm–persimmon–sassafras)			
30–59 years	50	30–59	
(elm–oak–hickory)			
60–99 years	100	60–99	Odum (1953)
(oak–hickory)			
100+	100+	100–500†	
(oak–hickory with possible succession to maple–beech)			
Maple–beech	150–200+	35–500+†	
Aspen	5	5–39	Essex and Gansner (1965)
Pine forest by age			
10–39 years	25	10–39	Odum (1953)
40+	25	40–100+	
Shrub areas	3	3–30	Bazzaz (1968), Beckwith (1954)
Residential habitat	..	1–100+	This paper
Marsh, natural	1,000+	600+	This paper
Marsh, man-made	3	3–100+	This paper
Prairie	10–15	10–30+	Booth (1941), Thomson (1940), Weaver (1961)
Ungrazed and fallow fields	..	1–10	This paper
Pastures	..	1–10	This paper
Hayfields	..	1–3	This paper
Small-grain fields	..	1	This paper
Row-crop fields	..	1	This paper

† Time based on sizes of largest trees in Illinois (Mohlenbrock, 1973) and growth rates for these species.

TABLE 2. Growth rates of representative tree species. This table is to be used to determine approximate ages of trees and replacement times for forests. Taken from Graber and Graber (1976)

Species	Annual growth rate†	Comment on use of growth rate	Reference and locality of reference data
Ash, green and white *Fraxinus pennsylvanica* and *F. americana*	0·22		Lorenz (1962) Central Illinois
Basswood *Tilia americana*	0·22		Chittenden and Robbins (1930) Southern Michigan
Beech, American *Fagus grandifolia*	0·12		Chittenden and Robbins (1930)
Box-elder *Acer negundo*	0·24		Lorenz (1962)
Cherry, black *Prunus serotina*	0·27		Conard (1918) Central Iowa
Cottonwood *Populus deltoides*	0·60 0·56 0·53	Use this rate for 4–15 inches DBH Use this rate for 16–25 inches DBH Use this rate for over 25 inches DBH	Williamson (1913) Mississippi Valley Gilmore *et al.* (1973) Southern Illinois
Cypress, bald *Taxodium distichum*	0·20 0·13	Use this rate for 4–40 inches DBH Use this rate for over 40 inches DBH	Mattoon (1915b) Maryland, Louisiana
Elm, American *Ulmus americana*	0·31 0·25 0·19	Use this rate for 4–10 inches DBH Use this rate for 10–15 inches DBH Use this rate for over 15 inches DBH	Lorenz (1962) Chittenden and Robbins (1930)
Elm, red *U. rubra*	0·49		Conard (1918)
Gum, sweet *Liquidambar styraciflua*	0·30		Gilmore *et al.* (1973) Southern Illinois
Hickory, shagbark *Carya ovata*	0·22		Conard (1918)
Maple, silver *Acer saccharinum*	0·45		Lorenz (1962) Conard (1918)
Maple, sugar *A. saccharum*	0·15 0·10	Use this rate for 4–14 inches DBH Use this rate for over 14 inches DBH	Chittenden and Robbins (1930)
Oak, black *Quercus velutina*	0·24 0·15 0·10	Use this rate for 4–10 inches DBH Use this rate for 11–15 inches DBH Use this rate for over 15 inches DBH	Vestal (unpublished) Southern Illinois Gevorkiantz and Scholz (1944) Southwestern Wisconsin

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Species	Rate†	Description	Reference
Oak, bur *Q. macrocarpa*	0·26	Use this rate for 4–10 inches DBH	Lorenz (1962)
	0·16	Use this rate for 11–15 inches DBH	Conard (1918)
	0·11	Use this rate for over 15 inches DBH	
Oak, pin *Q. palustris*	0·34		Vestal (unpublished) Southern Illinois
Oak, post *Q. stellata*	0·17		Vestal (unpublished) Southern Illinois
Oak, red *Q. rubra*	0·152		Robbins (1921) Missouri
Oaks *Quercus* spp.	0·16	Use this rate for 4–12 inches DBH	Gevorkiantz and Scholz (1944)
	0·128	Use this rate for 13–18 inches DBH	
	0·104	Use this rate for over 18 inches DBH	
Pine, loblolly *Pinus taeda*	0·30	Use this rate for 4–10 inches DBH	Forbes and Demmon (1929) Virginia, Florida, Texas
	0·25	Use this rate for 11–15 inches DBH	Arnold (1973) Southern Illinois
	0·20	Use this rate for over 15 inches DBH	
Pine, shortleaf *P. echinata*	0·29	Use this rate for 4–8 inches DBH	Mattoon (1915a) Western Arkansas
	0·25	Use this rate for 9–12 inches DBH	Arnold (1973)
	0·20	Use this rate for 13–17 inches DBH	Forbes and Demmon (1929)
	0·15	Use this rate for 18–20 inches DBH	
	0·10	Use this rate for over 20 inches DBH	
Pine, white *P. strobus*	0·23	Use this rate for 4–15 inches DBH	Lorenz (1962)
	0·12	Use this rate for over 15 inches DBH	Dwight (1926) Ontario, Canada
Sassafras *Sassafras albidum*	0·27		Rennels (1971) Central Illinois
Sycamore *Platanus occidentalis*	0·44		Vestal (unpublished) Gilmore *et al.* (1973) Southern Illinois
Walnut, black *Juglans nigra*	0·43	Use this rate for 4–15 inches DBH	Conard (1918) Losche (1973) Southern Illinois
	0·30	Use this rate for over 15 inches DBH	Lorenz (1962) Smith (1973) Central Missouri
Willow, black *Salix nigra*	0·54	Use this rate for 4–20 inches DBH	Lamb (1915) Arkansas
	0·46	Use this rate for 21–26 inches DBH	
	0·28	Use this rate for over 26 inches DBH	

† Given in inches. This figure divided into the diameter (in inches) of a tree will give the approximate age of the tree in years.

an example, let us consider the principal mode of dispersal. The extent of damage would be significantly greater if a disproportionate number of mammal- and gravity-dispersed guilds were extirpated while few wind-dispersed guilds were lost. Alternatively, the impact of the disturbance could be substantially mitigated were the converse to occur. This analysis, carried out for each division, gives an overview of the change in number and importance of the area's guilds. Damage can be determined by the ratio of the post-disturbance weighted guild total to the weighted total before the disturbance.

Predicting recolonization time or speed of recovery is primarily useful for examining the successional sequence of guilds invading heavily disturbed or denuded sites. Thus, we may make a relative determination of when to expect impacted species to re-establish. The extent of degradation will be variable dependent on the time replacement value of the pre-disturbance community. In general, early successional guilds such as the herbaceous, wind-dispersed, autogamous plants have a fast recovery time, while a late successional guild such as the woody, mammal-dispersed, insect-pollinated plants have a long recovery period. The speed of recovery for gross habitats can be estimated by the years of replacement time (Table 1). On heavily disturbed or denuded sites, where the soil is removed or substantially altered, a successional lead-in time must be added to the replacement time (Graber and Graber, 1976). These numbers provided a more quantitative estimation for the recovery time of specific guilds in each gross habitat.

The extent and state of decay of treefalls should at least be noted qualitatively, as these localized disturbances increase community diversity via spatial coexistence of successional seres (Margalef, 1962; Platt, 1975; Thompson, 1980) exhibiting a spectrum of reproductive and dispersal strategies (Forcier, 1975). Hence, localized disturbances represent an additional time component for replacement and may also increase the number of coexisting guilds.

Special attention should be given to dominant species in the area. Dominant woody species such as maple–beech, oak–hickory, or spruce–fir in their respective provinces should be surveyed to determine age structure and abundance (see Table 2 for growth rates of several woody species).

Mitigation of impact by using procedures to facilitate speedy recovery will reduce the replacement time. Eliminating practices that scrape off the top few inches of soil may reduce the impact to potentially resprouting perennials, as well as lessen the loss of small mammals (Severinghaus, pers. comm.). This would also prevent the removal of long-lived seeds from the area's soil seed bank (Cattelino et al., 1979). Avoiding soil compaction where possible would aid in re-establishment from the seed bank, as germination would be easier. On large impacted areas, it may be beneficial to leave small undisturbed habitat islands, if possible, to serve as seed and pollen sources and to promote animal activity, i.e. as dispersers and pollinators.

One problem area with this system is that it provides only a relative order of arrival. For example, I would expect the herbaceous, wind-dispersed, autogamous, annual guild to be one of the first guilds to invade an area. Alternatively, it would be difficult to predict whether the herbaceous, mammal-dispersed, autogamous annuals would precede or follow the herbaceous, bird-dispersed, insect-pollinated, perennial guild. Post-disturbance monitoring of these sites or similar refurbished areas will increase the system's predictive accuracy.

In conclusion, this system represents an ecological classification of vegetation useful for impact analysis and examining community structure. The system eliminates sub-jectivity and results in comparable interpretations of a site when surveyed by different

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AN ECOLOGICAL CLASSIFICATION FOR
FRESHWATER FISH SPECIES OF THE CONTERMINOUS
UNITED STATES

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Acknowledgements

Introduction

Environmental impacts are usually assessed on a species-by-species basis. When all the species present in the community are ascertained, the impact of a given activity is predicted for each species or group of species. Another course would be to divide species into groups that would be similarly affected by a given activity. The biological guild concept offers an avenue whereby such groupings can be made. A guild is defined as a group of species that exploit the same resource in a similar fashion (Root, 1967). We can use the guild concept to group species by their ecological requirements. Grouping species on the basis of how they exploit resources of several kinds, such as in an ecological classification, allows identification of species similarly affected by an environmental perturbation whose effect is known. In this report, we present the variables used to define ecological groups of freshwater fish species and the resulting classificatory scheme. We then demonstrate the use of this classification scheme to predict or explain changes in fish species populations following habitat alterations.

Explanation of Variables

Table 1 gives the environmental variables we judged to be of general ecological relevance with respect to freshwater fish species. Subdivisions of each environmental variable represent categories which can be used to codify differential exploitation of a resource by various freshwater fish species. The variables we selected are among those that many authors (Trautman, 1940; Sigler and Miller, 1963; Cross, 1967; Miller and Robison, 1973; Pflieger, 1973; Lagler, et al., 1975) include as the important variables by which fish segregate themselves into different habitats.

Water Body Morphology

The subdivisions of this parameter are: (1) estuarine areas; (2) large rivers and lakes; (3) medium-sized streams; and (4) headwaters, springs, and mountain streams. Estuaries are areas where salt and fresh waters meet. Large rivers are differentiated from medium-sized streams in that they are wide (50 m or more) and they flow throughout their length, never forming successions of rapids and pools, as medium-sized streams may do. Headwater streams are small (less than 5 m across), and may be intermittent. Mountain streams may have the morphology of either medium-sized streams or headwaters, but their waters are always cool and highly oxygenated. A fish species is placed into one of these categories on the basis of which type of water body it frequents most. Of all the parameters in our classification, this is the only one for which a given species has been placed in more than one

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Table 1. Environmental variables and subdivisions used to categorize
          the freshwater fishes of the conterminous United States.

Variable	Subdivisions
Water body morphology	Estuaries Large rivers and lakes Medium-sized streams Headwaters, springs, and mountain streams
Current	Required Not required
Turbidity	Tolerated Not tolerated
Structure	Preferred. Not preferred
Substrate	Rock Sand No preference
Food	Fish Invertebrates Detritus Omnivorous
Breeding sites	River channels Gravel shoals Nest Structure Eggs broadcast

subdivision. In other words, some species are categorized in more than one water body subdivision (e.g., carp are present in both large rivers and lakes, as well as in medium-sized streams).

Current

Subdivisions for this parameter are current required or current not required. A fish species is categorized as requiring current if it needs something that current provides (e.g., highly oxygenated water). These species may be able to live in areas without current, but they only thrive in areas affected by current. Species never found in lakes or ponds are assumed to require current. Species not requiring current may be found in areas with or without current.

Turbidity

Subdivisions of this parameter are turbidity tolerated or turbidity not tolerated. A species was classified as tolerant of turbidity if it can exist in locations characterized by long-term turbidity (more than a few weeks). We here characterize turbid water as having a Secchi disc depth of less than 10 cm. Non-tolerant species are those never found where long-term turbidity is the predominant condition.

Structure

The subdivisions are "structure preferred" and "structure not preferred." A species is classified as preferring structure if it is usually found near structure of some kind (e.g., macrophytes, submerged logs, or artificial reefs). Species are considered not to prefer structure if they are rarely found near structure, or if they are found near or away from structure in equal amount.

Substrate

Species are classified according to their preferences for rock bottoms or sand, or as not demonstrating such a preference. Species not having a preference were those found over a number of different substrate types; this group includes species found over silt.

Food

The subdivisions are invertebrate prey, fish, detritus, or omnivorous. Invertebrate prey includes macroinvertebrates (crayfish, etc.), benthic invertebrates, and zooplankton. Species with filter-feeding young and non-feeding adults (Ichthyomyzon) are placed in this category. Parasitic lampreys are placed in the fish-eating category. Almost all fish-eating species eat invertebrates after or during their larval stages. This change in diet is assumed in our classification. Detritus includes periphyton, substrate

particles, and sediment in the diet. Omnivorous species are those that eat food from all or some of the above categories.

Breeding Sites

These subdivisions are condensed from Balon (1975). They include: (a) river channels; (b) gravel shoals; (c) structure; and (d) eggs broadcast randomly. River channel spawners are those that require flowing river to spawn; their eggs usually roll on the bottom of the channel. Gravel shoal spawners include anadromous species such as salmon, as well as those species that live in gravel shoals. These forms usually require highly oxygenated water for their eggs to hatch. Nesting forms include those that actively construct a nest of some sort. Species requiring structure to spawn are those that spawn in vegetation, on sticks, or in crevices. This category also includes those forms that build nests out of structure, such as Gasterosteus aculeatus. The "eggs broadcast" category includes species that broadcast their eggs randomly over a variety of substrates. Species with floating eggs are in this group.

Classificatory Scheme

Figure 1 illustrates our classification scheme for freshwater fish of North America. This dendromatic representation is made to fit the fish species included in Eddy and Underhill (1979). An original dendrogram was constructed with the fish species of Missouri. For these species, Pflieger (1975) provided information that we evaluated before placing species in the classification scheme. Information on the Missouri fish species was verified with other references (Cross, 1967; Miller and Robison, 1973). After the classification was established, we attempted to assign species from a different fish fauna into the scheme. With information from Sigler and Miller (1963), we fitted the fish species of Utah to the classification. In the process, a few more categories were added--categories not filled by any species from Missouri (category 26 is an example).

In some cases, different subdivisions of a variable have been lumped. For example, category 18 combines the breeding site categories of eggs broadcast, nest, and structure. Category 22 lumps the food categories of fish and invertebrates. In general, this consolidation was done to avoid a proliferation of groups. Example species for each category are given in Table 2. For common names of these species, see Table 3. No interpretations should be drawn from the order in which the variables appear on the axis of the dendrogram. Those variables with two alternative choices were used to construct the initial subdivisions (branching points to the left of the dendrogram) after which those variables which had three or more alternatives were incorporated. This leads to a simpler representation of the classification.

The construction of the classification scheme is instructive in terms of its future applications. We found it necessary to add categories to fit fishes of Utah successfully into the classification. Since in the process of developing the scheme, only 200 of the 700 freshwater fishes of North America
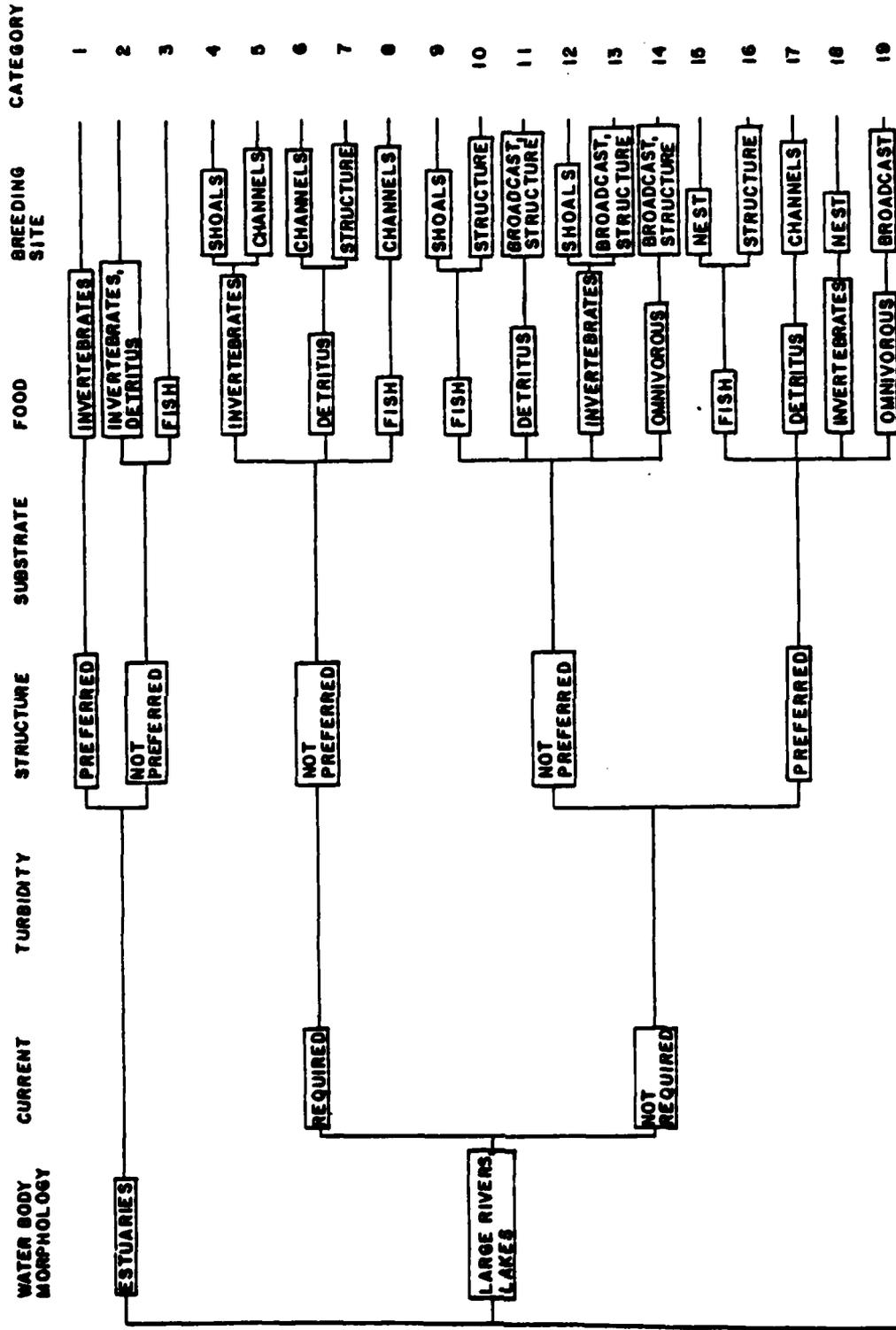
Figure 1. Ecological classification for the freshwater fish species of the conterminous United States. Variables and subdivisions are explained in the text.

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Figure 1. (Cont'd).

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Figure 1. (Cont'd).

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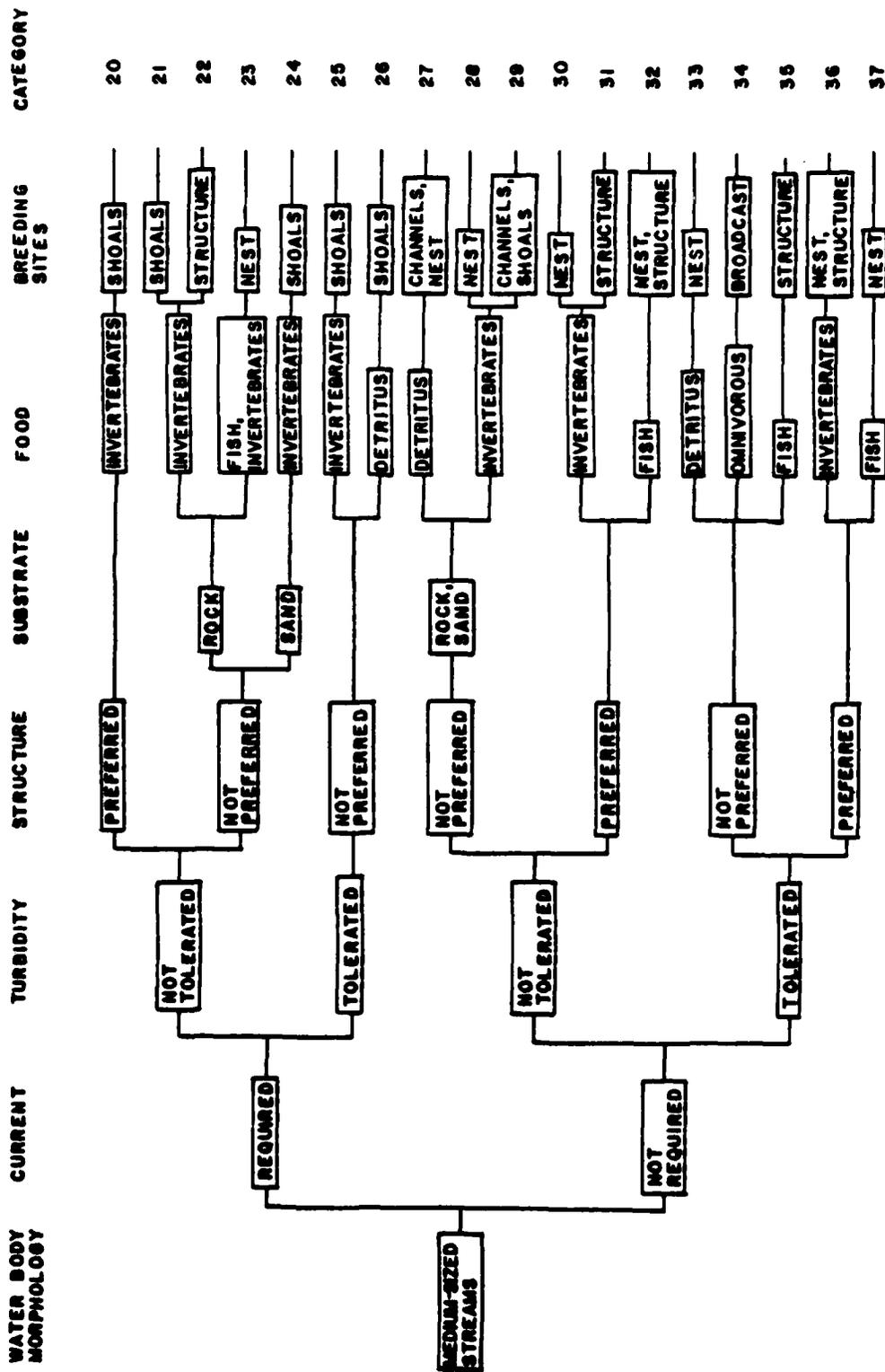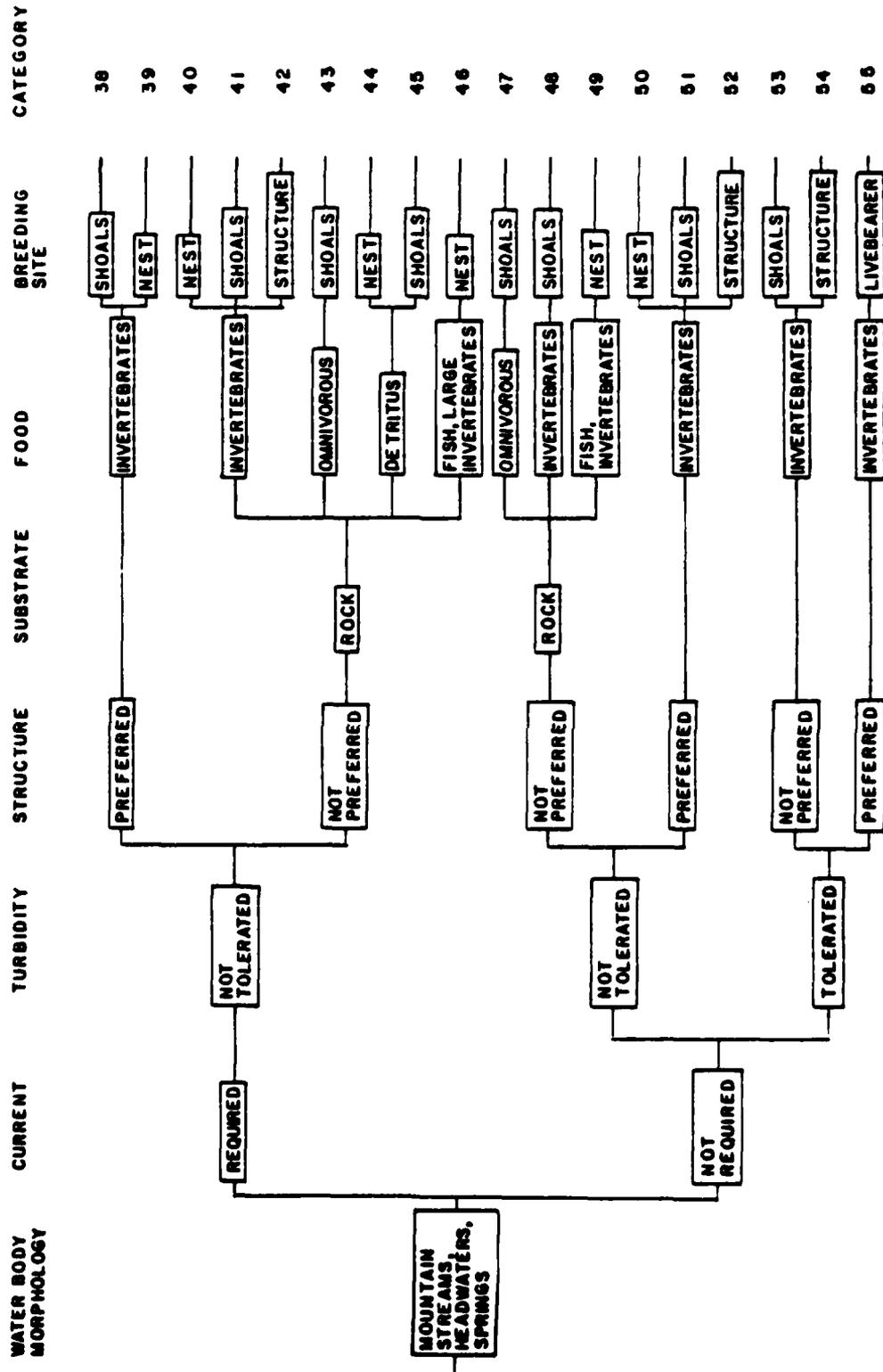
Table 2. Example species arranged by subdivision, according to numbering in Figure 1.

Category	Species	Category	Species
1	Syngnathus scovelli	29	Labidesthes sicculus
2	Anchoa mitchilli	30	Lepomis symmetricus
3	Megalops atlantica	31	Notropis emiliae
4	Cycleptus elongatus	32	Amia calva
5	Scaphirhynchus platorynchus	33	Pimephales promelas
6	Hybognathus placitus	34	Ictalurus melas
7	Carpiodes velifer	35	Lepisosteus osseus
8	Alosa chrysochloris	36	Etheostoma gracile
9	Morone mississippiensis	37	Pomoxis annularis
10	Lepisosteus platostomus	38	Percina sciera
11	Carpiodes carpio	39	Noturus flavater
12	Hiodon alosoides	40	Fundulus catenatus
13	Dorosoma cepedianum	41	Etheostoma blennioides
14	Aplodinotus grunniens	42	Notropis galacturus
15	Lepisosteus oculatus	43	Phoxinus erythrogaster
16	Micropterus salmoides	44	Campostoma anomalum
17	Ctenopharyngodon idella	45	Dionda nubila
18	Lepomis microlophus	46	Semotilus atromaculatus
19	Lota lota	47	Catostomus commersoni
20	Notropis boops	48	Ichthyomyzon fossor
21	Notropis volucellus	49	Salmo gairdneri
22	Notropis whipplei	50	Ambloplites rupestris
23	Micropterus punctulatus	51	Thymallus arcticus
24	Ammocrypta vivax	52	Etheostoma microperca
25	Phenacobius mirabilis	53	Catostomus platorynchus
26	Catostomus discobolus	54	Fundulus olivaceus
27	Pimephales notatus	55	Gambusia affinis
28	Lepomis megalotis		

Table 3. Scientific and common names for species referred to in the text. Names follow Bailey, et al. (1970).

Scientific name	Common name
Alosa chrysochloris	Skipjack herring
Ambloplites rupestris	Rock bass
Amia calva	Bowfin
Ammocrypta vivax	Scaly sand darter
Anchoa mitchilli	Bay anchovy
Aplodinotus grunniens	Freshwater drum
Campostoma anomalum	Stoneroller
Carpiodes carpio	River carpsucker
Carpiodes velifer	Highfin carpsucker
Catostomus commersoni	White sucker
Catostomus discobolus	Bluehead sucker
Catostomus platyrynchus	Mountain sucker
Ctenopharyngodon idella	White amur (grass carp)
Cycleptus elongatus	Blue sucker
Cyprinus carpio	Carp
Dionda nubila	Ozark minnow
Dorosoma cepedianum	Gizzard shad
Dorosoma petenense	Threadfin shad
Etheostoma blennioides	Greenside darter
Etheostoma gracile	Slough darter
Etheostoma microperca	Least darter
Etheostoma radiosum	Orangebelly darter
Etheostoma spectabile	Orangethroat darter
Fundulus catenatus	Northern studfish
Fundulus kansae	Plains killifish
Fundulus notatus	Blackstripe topminnow
Fundulus olivaceus	Blackspotted topminnow
Gambusia affinis	Mosquitofish
Gasterosteus aculeatus	Threespine stickleback
Hiodon alosoides	Goldeye
Hybognathus nuchalis	Silvery minnow
Hybognathus placitus	Plains minnow
Hybopsis aestivalis	Speckled chub
Hybopsis storeriana	Silver chub
Ichthyomyzon fossor	Northern brook lamprey
Ictalurus furcatus	Blue catfish
Ictalurus melas	Black bullhead
Ictalurus punctatus	Channel catfish
Ictiobus bubalus	Smallmouth buffalo
Ictiobus cyprinellus	Bigmouth buffalo
Labidesthes sicculus	Brook silverside
Lepomis cyanellus	Green sunfish
Lepomis macrochirus	Bluegill
Lepomis megalotis	Longear sunfish
Lepomis microlophus	Redear sunfish

Table 3 (cont'd)

Scientific name	Common name
Lepomis symmetricus	Bantam sunfish
Lepisosteus oculatus	Spotted gar
Lepisosteus osseus	Longnose gar
Lepisosteus platostomus	Shortnose gar
Lepisosteus spatula	Alligator gar
Lota lota	Burbot
Megalops atlantica	Tarpon
Menidia audens	Mississippi silverside
Micropterus dolomieui	Smallmouth bass
Micropterus punctulatus	Spotted bass
Micropterus salmoides	Largemouth bass
Morone chrysops	White bass
Morone mississippiensis	Yellow bass
Morone saxatilis	Striped bass
Moxostoma erythrurum	Golden redhorse
Notemigonus crysoleucas	Golden shiner
Notropis atherinoides	Emerald shiner
Notropis bairdi	Red River shiner
Notropis boops	Bigeye shiner
Notropis buchanani	Ghost shiner
Notropis chrysocephalus	Striped shiner
Notropis emiliae	Pugnose minnow
Notropis fumeus	Ribbon shiner
Notropis galacturus	Whitetail shiner
Notropis lutrensis	Red shiner
Notropis potteri	Chub shiner
Notropis shumardi	Silverband shiner
Notropis stramineus	Sand shiner
Notropis venustus	Blacktail shiner
Notropis volucellus	Mimic shiner
Notropis whipplei	Steelcolor shiner
Noturus flavater	Checkered madtom
Percina caprodes	Logperch
Percina sciera	Dusky darter
Phenacobius mirabilis	Suckermouth minnow
Phoxinus erythrogaster	Southern redbelly dace
Pimephales notatus	Bluntnose minnow
Pimephales promelas	Fathead minnow
Pimephales vigilax	Bullhead minnow
Polyodon spathula	Paddlefish
Pomoxis annularis	White crappie
Pylodictis olivaris	Flathead catfish
Salmo gairdneri	Rainbow trout
Scaphirhynchus platorynchus	Shovelnose sturgeon
Semotilus atromaculatus	Creek chub
Syngnathus scovelli	Gulf pipefish
Thymallus arcticus	Arctic greyling

have been incorporated into this classification, it is almost certain that a few additional categories will have to be added as new species are evaluated. The classification of some species is based on extrapolations, for many species have not been well studied, especially in terms of their reproductive classification. As additional information becomes available, the placement of some species may change. This classificatory scheme should not be regarded as a static, finished object. As new information comes to light and new species are placed in the classification, the classification scheme must be allowed to change.

Examples

In the following examples, we have used presence of species representing a given classification, or relative abundance or rarity of species in given categories, to identify changes caused by man-made habitat alterations. In these cases we have not compared actual numbers of individuals (within each category) between locations. Enumeration of individuals within each category and subsequent comparison of areas assumes equal sampling efforts or equal sampling areas between the areas being compared. Often the data available do not conform to these assumptions. If quantitative data on fish communities are available, this method of categorizing species may be used as an additional tool. Our analysis below is basically qualitative, and the following examples should be judged in this light.

Lake Texoma and Red River Fish Fauna

About 40 years ago, Denison Dam backed up the Red and Washita Rivers to form Lake Texoma between Oklahoma and Texas. Collections from the Red River drainage and Lake Texoma are housed in the University of Oklahoma Stovall Museum. We used these collections to assess the fish species composition of the Red River and Lake Texoma. The fish species characteristic of the river and the lake are represented in Figure 2. Some variables do not appear in this classification, for they do not differentiate among fish species of this drainage. For example, most of the fish inhabiting the Red River are at least moderately tolerant of turbidity. The species found in the river and the lake are listed in Table 4.

Damming of the Red River and the elimination of current should exclude those species that require current. These are the species in categories 4, 5, 6, and 8. In fact, most of these species are not present in the lake. Exceptions are *Notropis potteri* and *Percina caprodes* (both in category 5), which are found in Lake Texoma in small numbers. The forms in categories 9 through 17 thrive in the lake. They are also found in the Red River above and below the lake, demonstrating that either current is tolerable to them, or pools and backwaters provide locations with no current. *Polyodon spathula* and *Lepisosteus spathula*, once present in the lake, are now absent or extremely reduced due to commercial fishing.

Our classification would have allowed us to predict that fishes in categories 4 through 8 would not have done well after the river was dammed. If the Washita River and the Red River were dammed above Lake Texoma, we would predict that those species requiring upstream shoals to spawn would be blocked
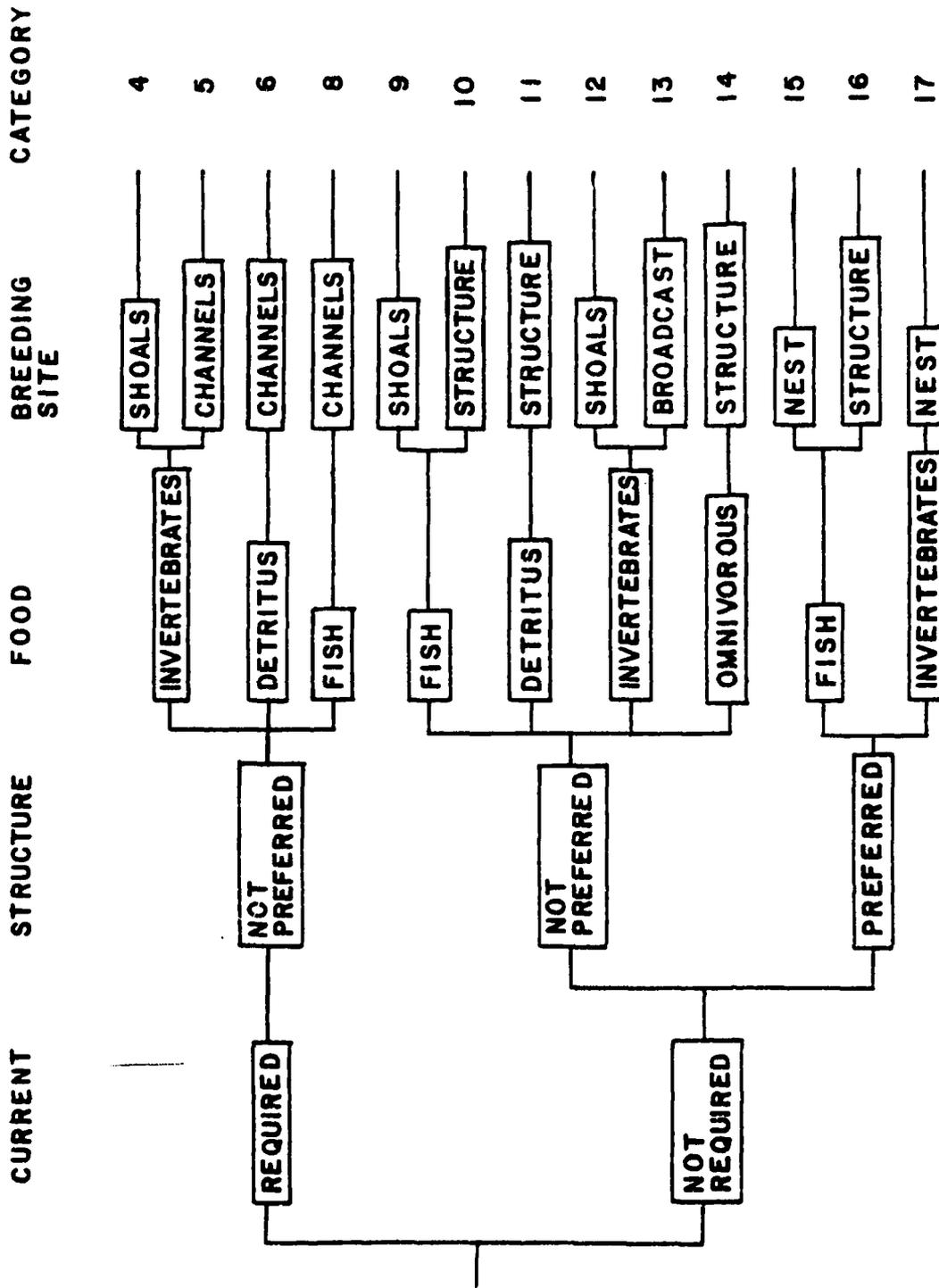
Figure 2. Ecological classification for the fish species inhabiting the Red River and Lake Texoma in Oklahoma and Texas.

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Table 4. Fish species of Lake Texoma and the Red River drainage in Oklahoma and Texas, arranged by categories identified in Figure 2.

Category	Species
4	*Cycleptus elongatus*
5	*Scaphirhynchus platorynchus*, *Hybopsis aestivalis*, *Notropis bairdi*, *N. potteri*, *N. shumardi*, *Percina caprodes*
6	*Hybognathus nuchalis*, *H. placitus*
8	*Alosa chrysochloris*
9	*Morone chrysops*, *M. saxatilis*
10	*Lepisosteus osseus*, *L. platostomus*, *L. spatula*
11	*Ictiobus bubalus*, *Capriodes carpio*
12	*Polyodon spathula*, *Hiodon alosoides*
13	*Notropis atherinoides*, *N. buchanani*, *N. lutrensis*, *N. venustus*, *Pimephales vigilax*, *Menidia audens*, *Dorosoma cepedianum*, *D. petenense*, *Hybopsis storeriana*
14	*Cyprinus carpio*, *Notemigonus crysoleucas*, *Ictiobus cyprinellus*, *Ictalurus furcatus*, *I. punctatus*, *Pylodictis olivaris*, *Aplodinotus grunniens*
15	*Micropterus salmoides*, *Pomoxis annularis*
16	*Lepisosteus oculatus*
18	*Lepomis cyanellus*, *L. macrochirus*, *L. megalotis*, *L. microlophus*

from them and would suffer population decreases. These species are those in categories 9 and 12. The damming of the Washita River is in fact being Figure 2 planned, and if this happens, will undoubtedly severely affect the populations of <u>Morone saxatilis</u> and <u>M. chrysops</u>, which spawn in the Washita River.

Glover River Clearcutting Effects

The Glover River is a medium-sized stream that flows through pine plantations in southeastern Oklahoma (McCurtain County). Areas of pine have been clearcut at a number of locations along the river, and there has been resultant siltation of the stream. We seined the Glover River at two locations in July of 1980. The first location, associated with extensive clearcuts, was 8 river km (5 mi) upstream from the bridge for state roads 3 and 7. The clearcuts associated with this location were approximately 3 years old. The second location, apparently unaffected by clearcuts, was above a low-water bridge at the town of Glover. This was 9.7 km (6 mi) below the first location. At both locations there were riffles and pools, structure was available, the water was clear, and both sand and rock substrates were present. At the first locality, the rock substrate in pools was overlain by a layer of silt. Fish were collected by seine (3.7 m long, 2 m deep, 3-mm mesh). The species collected at both sites are given in Table 5.

No differences are readily apparent between the locations, on the basis of presence or absence of categories. Categories 24 and 37 were represented at the second location and not at the first. However, both these categories were poorly represented at the second location. Only categories 20 and 28 showed large differences in numbers of individuals collected in the two locations. At both locations, category 20 was the most important. In sum, few obvious differences can be detected between the two locations.

Siltation may not adversely affect adult fish, since most species are quite mobile. Siltation may heavily affect eggs, which smother if covered with silt. It may be that fish population changes associated with siltation would only be apparent after several years, when the failure of given year classes of fish would become apparent. When silted areas are not extensive, migration from nearby, unaffected, areas may keep fish populations high in the silted areas. While this preliminary example did not show substantial differences between the locations, more intensive and extensive studies would of course be needed to fully evaluate the influence of clearcutting on fish populations.

Channelization of Kickapoo Sandy Creek

Kickapoo Sandy Creek is a small creek feeding into the Washita River in Murray County, Oklahoma. One section of this stream has been channelized. Channelization involved removal of trees and shrubs from the banks, grading and stabilization of the banks, and widening the stream channel. We seined two locations on Kickapoo Sandy Creek in July of 1980. Location 1 had been channelized. There was no current, the stream having dried up into a series of pools. No structure was available in the pools or in the dried-up channel. The substrate was sand. Location 2 had not been channelized. The

Table 5. Fish species collected from the Glover River, McCurtain County,
Oklahoma. Two locations were collected: (1) associated with
clearcuts and (2) not associated with clearcuts. In parentheses
following each species name is: the number collected at location
1 / the number collected at location 2.

Category	Species
20	Notropis boops (111/62), Percina sciera (0/10)
21	Notropis chrysocephalus (0/2), Etheostoma radiosum (5/4), E. spectabile (0/7)
22	Notropis whipplei (38/47)
23	Micropterus dolomieui (1/0), M. punctulatus (0/1)
24	Notropis fumeus (0/3)
26	Campostoma anomalum (14/17)
28	Lepomis megalotis (12/36)
29	Moxostoma erythrurum (4/0, Labidesthes sicculus (1/0)
33	Pimephales notatus (2/2)
34	Ictalurus melas
36	Fundulus notatus (3/3), Lepomis cyanellus (2/2), L. macrochirus (2/2)
37	Micropterus salmoides (0/1)

stream was again dried into pools and the substrate was sand. Structure (dead branches) was available in the pools. We consider the fauna of this creek to be representative of the medium-sized stream division, despite the small size of the creek (it is essentially a headwater type of stream). This is because the fauna is derived from the Washita River fauna, which is in the medium-sized stream division. The ecological classification of the species is given in Figure 3. The species collected and their numbers are given in Table 6.

Channelization usually increases the flow rate in a stream, and the channelization process usually includes removal of obstructions (structure) in the stream bed. The ecological categories represented at the two locations reflect the differences in flow and structure availability. At location 1, category 26 was represented, while it was not at Location 2. Species in this category require current. One category (37) was represented at Location 2, and not at Location 1. Species in category 3 prefer structure. The other categories represented reflect species preferences for current or structure. Categories 26 and 34 (not preferring structure) predominated in the channelized portion. We have not counted Gambusia affinis in our assessment of these locations. This species tends to multiply in isolated, predator-free pools. Category 36 is abundantly represented in the channelized portion because of the special conditions leading to proliferation of Gambusia affinis in the channelized portion. Location 2 contains a number of forms not preferring structure, but forms preferring structure were more numerous in the unchannelized portion. The habitat alteration of this stream (removal of structure and ensuring water flow) is reflected in the species present in the two locations.

Table 6. Fishes of Kickapoo Sandy Creek, Murray County, Oklahoma. Categories follow numbering in Figure 1. Two locations were collected: location 1 channelized and location 2 not channelized. In parentheses following each species name is: the number collected at location 1 / the number collected at location 2.

Category	Species
26	Campostoma anomalum (12/0)
34	Notropis lutrensis (140/28), N. stramineus (6/0), Carpiodes carpio (0/1), Ictalurus melas (0/1), Fundulus kansae (100/0)
36	Notemigonus crysoleucas (0/1), Gambusia affinis (188/34), Lepomis cyanellus (8/0), L. macrochirus (2/2), L. megalotis (0/12), L. microlophus (0/5)
37	Micropterus salmoides

Conclusions

This classificatory scheme should be seen as a useful tool for organizing information from field collections, species lists, and other enumerations of species usually supplied in environmental impact analyses. The examples illustrate that predictions of population trends can follow from the classification of species according to their ecological requirements. This method is useful for qualitatively sampled fish populations, as was pointed out previously. Comparisons of locations using techniques requiring enumeration of species and individuals, such as diversity or equitability indices, assume equal sampling efforts, etc.

This classificatory scheme must be modified as new information becomes available for different species. Attempted classification of certain species will point up areas where more research is needed. Finally, classification of species into ecological groups will allow this information to be available to non-ichthyologists, such as the people who normally must make decisions from the conclusions presented in environmental impact analyses.

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