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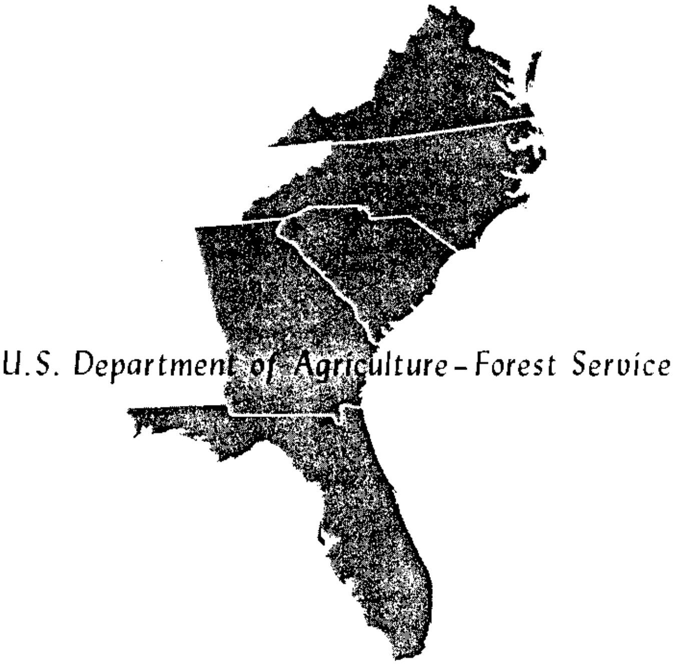
FOREST DIVERSITY
New Concepts and Applications

by
Stephen G. Boyce
and
Noel D. Cost



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Stephen G. Boyce, Chief Forest Ecologist

and

Noel D. Cost, Resource Analyst
Asheville, North Carolina

Abstract.--The National Forest Management Act of 1976 requires that plans provide for the diversity of plant and animal communities to meet multiple-use objectives and, to the degree practicable, the preservation of tree species indigenous to particular forest regions.

The purpose of this paper is to define "diversity" as it applies to forest management and to discuss concepts relative to maintaining a desired stability of forest plant and animal life. Data presented support the contention that the monitoring of the natural succession of forest stands is useful for making management decisions, assuring diversity, and for keeping multiple-use objectives congruent with consumer attitudes for social and economic benefits.

KEYWORDS: Diversity, renewable resources, multiple-use, stability.

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1. INTRODUCTION

1.1 The Issues

Public concern for maintaining certain kinds of diversity in renewable resources is expressed in the National Forest Management Act of 1976 (90 Stat. 2949; 16USC1600). The Act requires that plans provide for the diversity of plant and animal communities to meet multiple-use objectives and specifies that steps be taken to preserve the diversity of existing tree species. To meet these provisions, the development of alternative management plans and definitions is necessary.

Forest managers have not previously defined diversity of renewable resources as an objective for management (Ford-Robertson 1971; Smith 1962;. Forbes 1961), nor is there a useful definition in biological literature. Management for diversity to meet multiple-use objectives therefore is a new direction for forestry.

Obviously, the first requirement was to develop an operational definition for diversity of renewable resources. Section 2.1 provides this definition.

In section 2.2 we show how the diversity of renewable resources can be related to the availability of one or more benefits. In section 2.3 our analysis leads to the conclusion that increasing diversity of species does not beget stability of forest communities. In section 2.4 we illustrate how Shannon-type indices are confounded and, thus, cannot be used to develop relationships for use in management decisions. In section 2.5 we show how to monitor constraint in the distribution of habitats. And, we explain how constraint in the distribution of habitats may limit the livelihood for endemic species.

In section 3 we show how to compare the diversity of tree species in national forests and in a large surrounding region. The same method can be used for other parts of the Nation. We show that direct comparisons of lists of species, and possibly some other elements such as diameter class, are useful for management decisions.

In section 4 we use lists of forest types by stand condition classes to illustrate methods for direct comparisons of the diversity of plant and animal communities. We also illustrate ways to anticipate changes in the diversity of communities with different modes of management and changes under natural forces unaffected by man.

In section 5 we illustrate how diversity and benefits may be integrated to simultaneously analyze, estimate, and specify the consequences of alternative plans for multiple benefits. We describe how diversity is monitored and how data from periodic inventories can be used to keep multiple-use objectives congruent with consumer attitudes toward social and economic benefits from forests.

2. DEFINITION, CONCEPTS, AND THE SHANNON-TYPE OF DIVERSITY INDICES

2.1 An Operational Definition for the Diversity of Renewable Resources

The kinds of coexistent animals, plants, and microorganisms vary within and among forest stands. As time progresses, these renewable resources change in kind and in relative proportions from place to place. These variations are recognized as "diversity," which is the condition of being different. The classification, measurement, and control of the elements that make up diversity of forests and ranges are activities associated with managing renewable resources. It is the proportional distribution of diverse situations, such as different combinations of species and different habitats, that determines the availability of timber, wildlife, range production, recreation, streamflow, esthetics, and other benefits (Boyce 1977, 1978; Siderits and Radtke 1977; Flood and others 1977).

The development and the maintenance of certain differences among forest stands is an important principle for managing forests. For example, forest animals require various kinds and combinations of stand conditions in all seasons. The greater the difference, the greater is the opportunity for food and shelter (U.S. Dep. Agric., Forest Service 1971). For an increased flow of water without excessive sediment, the management technique is to establish a variety of age classes of stands (Douglass and Swank 1976). A sustained harvest of timber is also based on maintaining different age classes from regeneration to harvest (Smith 1962).

Classification, mensuration, and statistical sampling techniques have been developed to distinguish and measure meaningful differences in the elements of communities (Forbes 1961; Husch and others 1972). These elements include species of trees, forest types, animal and plant populations, volumes of timber, amounts of browse and hard mast, age classes of stands, site index, and stand condition classes (U.S. Dep. Agric., Forest Service 1967). Thus, these differences, which are viewed as diversity of renewable resources, are operationally defined. Criteria are specified so that one species of animal can be consistently distinguished from another; continuums, such as tree diameters and stand conditions, can be separated into meaningful classes; and whether some observed difference is meaningful for management decisions can be statistically determined.

An operational definition of the diversity of renewable resources is, in brief, the meaningful differences in the elements of biological communities.

The operational criteria are:

a. Identify which elements of the community are being considered (i.e., tree species, bird species, forest types, stand conditions, age classes).

b. Specify measurements or characteristics which evaluate or distinguish elements (i.e., differences between species, measurements for classes of a continuum).

c. Describe how the differences between elements are meaningful. for management decisions (i.e., stand condition classes and the livelihood for a plant or animal, sizes of trees, and the potential for wood products).

Our definition of "diversity" is essentially the same as provided in most dictionaries. Thus, we are not proposing an uncommon meaning. The operational criteria provide the scientific basis for different people to repeat observations and measurements and, thus, provide scientific credibility for management decisions (Bridgman 1927).

2.2 The Relation of Diversity to Benefits

In this section we illustrate how diversity of elements of renewable resources can be related to the availability of one or more benefits. Such relationships are useful for considering alternative management plans and for choosing management actions. A well-known concept for providing a timber benefit is used to illustrate the relation of diversity of resources to a benefit.

Timber can he harvested only from stands that have trees large enough to meet a definition for timber. We define "timber" as trees 11 inches d.b.h. and larger and define a mature timber stand as one with half of the dominant and codominant trees qualifying as timber. If one has a forest with no timber, no timber benefits can be derived immediately. If all the stands in the forest are mature, the maximum timber benefit can be achieved in the shortest time. However, if one wants an annual timber benefit over a long period of time, then it is necessary to bring about a diversity of age classes and areas for each stand (Smith 1962). If one chooses the difference in the age classes to be 1 year, then the maximum area of stands for each age class equals the forest area divided by the time required for stands to become mature. Other diverse combinations are possible.

The diversity of stand area and age classes provides benefits other than timber. For example, a certain amount of livelihood for deer is provided by browse in the seedling years, by some hard mast as the stands approach maturity, and by cover in the sapling years (U.S. Dep. Agric., Forest Service 1971). During the seedling years the proportions of certain kinds of spiders increase, and as the stands age, the proportions of other kinds of spiders increase (Coyle, In press). If the diversity of annual age classes is changed, the timber benefit, as well as the potential livelihood for deer, the species of spiders, and other benefits will change. It is the state of organization of the forest (in this example the diversity of annual age classes) that determines the availability of multiple benefits.

This example illustrates one way diversity of specified elements of renewable resources can be used to make management decisions about the availability of specified benefits. It also illustrates the theory for multiple benefits, i.e., "the kinds and proportions of states of organization (habitats) determine the kinds and proportions of human benefits available from a forest" (Boyce 1977).

We can now consider how a reduction in the proportion of habitats reduces the availability of benefits. Consider first a random distribution of 80 age classes, each differing by 1 year. Such a distribution can be maintained by regulating the rate of harvest and the size of openings. Without a scheduled harvest and opening size, the larger trees increase in size and constrain both the size of openings and the proportion of stands in the younger age classes. In time the younger stands represent less of the forests. Correspondingly, benefits related to stands in the younger age classes decline, affecting the diversity of habitats.

Now, if we take appropriate action to increase the size of stands and the proportion of stands in the younger age classes, both the diversity of habitats and the availability of certain benefits increase. Not only can timber be harvested periodically, hut also a livelihood is provided for an increased number of species. From Coyle's (In press) research, we can expect to provide a livelihood for the largest number of species when all of the 1-year age classes are present. This leads us to another useful concept about diversity: an increase in the diversity of habitats increases the potential livelihood for diverse kinds of organisms.

Much of the evidence for this concept comes from studies of the evolution, migration, and extinction of plants and animals. As illustrated by numerous examples (Dobzhansky and others 1977; Mayr 1970; Harper 1977; Stebbins 1950, 1974), regions having many different kinds of habitats are more likely to have greater diversity of genotypes than regions with a few kinds of habitats. This fact is supported also by evidence that organisms with chromosomal variations are more likely to survive in transition areas between different habitats than in a large uniform habitat. This concept is used as a basic principle in the evaluation of habitats for wildlife (Hair, In press; Siderits and Radtke 1977; Flood and others 1977). If one is dealing with a specific species and certain habitat requirements are known, then the operational criteria for diversity can be specified.

Consider, for example, deer in a hardwood forest in the Southern Appalachians. In this forest the habitat value for deer is high when many seedling stands are interspersed in an area which has substantial stands of large pole and mature sawtimber. Seedling stands contribute soft mast and forage, while 10-inch poletimber and mature timber are producers of hard mast. The livelihood for deer rises as the proportion of area in seedling habitat increases up to about 7 percent of the total area and as mast-producing timber increases to about 20 percent of the area. These are assumed to be optimum proportions within the practical limitations of multiple-use management. Deer often use seedling browse more effectively when it occurs in openings less than 10 acres in size. As the opening size increases beyond about 30 acres, the utilization of the forage declines.

These relationships, which indicate diversity in the components of deer habitat, can be expressed in relatively simple charts (figs. 1, 2, and 3). On the

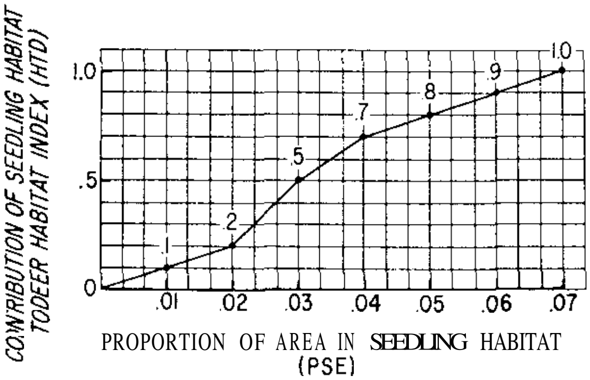

Figure 1.--Seedling habitats contribute soft mast and forage far deer (Boyce 1977).

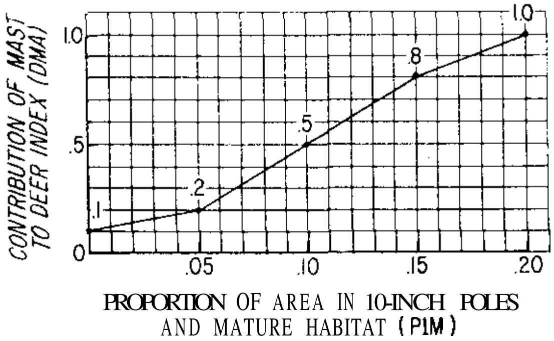

Figure 2.--Ten-inch pole and mature timber stands contribute hard mast far deer (Boyce 1977).

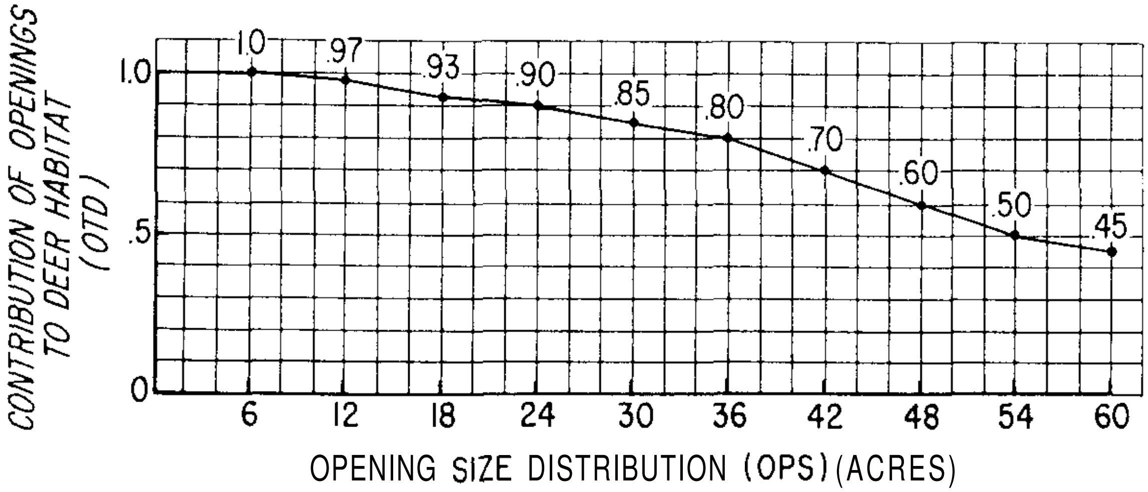

Figure 3.--Deer often use seedling browse more effectively when it occurs in openings of less than 10 acres (Boyce 1977).

verticle axis, the relative livelihood for deer is indicated by a scale of 0 to 1. For these examples, the product of the values that indicate the amount of browse, the amount of hard mast, and the size of openings, gives a combined index for some specific area. The diversity of forest elements, in this case the proportion of area in seedlings, large pole and mature timber, and opening size, can be used by forest managers to decide how alternative management actions may affect the livelihood for deer.

When one is dealing with a large number of species and an infinite number of differences in habitats, it is impractical to attempt to specify the operational criteria for each situation. One then relies on the concept that an increased diversity of habitats increases the potential livelihood for diverse kinds of organisms. A quantitative way to relate this concept to alternative management actions is discussed in section 2.5.

We use timber and wildlife benefits as illustrations, because the examples are widely known. The methods are readily applicable to esthetic, social, economic, and other benefits for which the elements of forest communities can be related. Thus, by knowing how management actions change diversity in the elements of forest communities, one can compare the consequences of alternative management plans.

2.3 Diversity of Species Does Not Add to the Stability of Communities

In this section we review the widely published concept that increasing diversity of species in communities begets stability. It is essential that we analyze this concept because it is often used to interpret consequences of actions to manage renewable resources (Cody and Diamond 1975; van Dobben and Lowe-McConnell 1975). Our analysis leads to the conclusion that unmanaged forests are nonequilibrium, aimless systems in which the diversity of species is a consequence of the dynamics of individualistic systems (Boyce, In press). We find no substantial evidence that increasing diversity of species begets stability of forest communities.

At the First International Congress for Ecology (van Dobben and Lowe-McConnell 1975), a primary concern was whether diversity of species contributed to stability of ecosystems. This meeting continued discussions that began in the late 1800's. Early studies of plant and animal species suggested slow rates of speciation and extinction and suggested that evolution increased diversity of species. A concept, not accepted by all biologists, was that the drift of evolution was toward diversity and complexity of individuals, which eventually resulted in relative stability in both the numbers of species and individuals (Watt 1966). Recently, the concept has been revived and there is widespread interest in diversity and the stability of communities.

In the literature the word "diversity" is frequently confused with the phrase "diversity index." Authors often define diversity by a mathematical expression that is a diversity index (Pielou 1977). Squiers and Wistendahl (1977) and Christensen (1977) distinguished between diversity as difference and diversity index as a dimensionless number. Harper (1977) uses diversity as difference and does not use diversity index. Odum (1971), Whittaker (1972), Pielou (1977), Peet (1974), and Auclair and Goff (1971) seem to use diversity and diversity index interchangeably. May (1976, page 158) argues for describing communities in terms of the elements of diversity rather than condensing information into diversity indices.

In his book on geographical ecology, MacArthur (1972) discusses the principle of community stability in some detail, presents a theory of species diversity, and develops a formula for indicating the amount of diversity in species. In a recent book dedicated to Robert MacArthur (Cody and Diamond 1975), a number of ecologists discuss the various concepts of diversity. One of the concepts propounded by MacArthur and his colleagues was that species diversities on continents should approach steady states. Furthermore, diversity was thought to be related to rates of evolution (MacArthur 1972; Cody and Diamond 1975). Diversity was used to provide explanations of adaptive radiation, to substantiate the community stability hypothesis, and to describe latitudinal differences in populations. The theory of species diversity and community stability (MacArthur 1972) became a vital force for a number of students of evolutionary ecology and biogeography (Cody and Diamond 1975).

Rates of evolution, migration, and extinction of species obviously affect the diversity of species in forests (Harper 1977). Stebbins (1950, 1974) described how these variables affect the diversity of flowering plants. He did not report evidence that increased diversity of species resulted in increased rates of evolution, migration, and extinction. For example, Stebbins presented no evidence for faster rates of speciation in the highly diverse tropical forests than for the less diverse temperate forests. Rather, evidence suggests that chromosomal variations are more likely to survive in a mosaic of diverse habitats than in an equal area with a uniform habitat (Dobzhansky and others 1977). Similar relationships are described by Mayr (1970) for animals.

The concept of increasing community stability with increasing diversity was strongly criticized by Hairston and others (1968). Loucks (1970) noted that long-term stability reduces diversity. In a recent symposium (Various authors 1970) there was no general agreement on the meaning of stability or on the relationship between stability and diversity. Hill (1973) concluded that diversity, as measured by the Shannon function (Shannon and Weaver 1949), was simply a continuum of index values relating number of species to abundance of individuals. Hill (1973) suggested there was no particular biological merit in using the index; it is another way to illustrate differences in numbers of species and the relative distribution of species for a community.

One difficulty in relating increased diversity of species with increased stability of communities is the lack of any general agreement on how to recognize and quantitatively determine when a community is stable. For a number of subjective definitions of community stability, see MacArthur (1972), Stebbins (1974), Odum (1971), Cody and Diamond (1975), and van Dobben and Lowe-McConnell (1975). Alternatively, Kowal (1971) discusses the significance of stability as an indicator of the behavior of models for ecosystems and as a variable in the biological structure of real communities. Most models are expected to exhibit system stability, not "blow up" in time. Some ecologists expect real communities to exhibit also system stability, to achieve, retain, and return to some preconceived state after a perturbation. Kowal (1971) considers both forms of stability to depend on definitions.

In a recent paper, Odum (1975) defined optimum diversity as a function of the quality and quantity of energy flowing through a system. He says too much, as well as too little, diversity may be destabilizing. Odum does not tell how one can know when diversity is optimum. He urges caution in the use of diversity as a property of stable natural systems, and accordingly, as a desirable feature for the systems of man.

Orians (1975), reviewed more than 50 papers dealing with diversity, stability, and maturity in natural ecosystems. His conclusion is that researchers are unlikely to find general relationships that support the assumptions: succession generates diversity of species and diversity of species enhances the stability of community.

May (1976, page 158) discusses the assumption that increased complexity, which usually means more species, more interactions, and more differences in the elements of a community, increases stability. With the use of mathematical techniques, May (1976) concludes that large, unprecedented perturbations by man may be more traumatic for complex systems than for simple ones. He suggests that this inverts the naive view that "complexity begets stability.'' May suggests that there is no advantage in attempting to preserve, or even create, complex systems as buffers against man's importunities (May 1976, page 162).

Whittaker (1975) questioned a simple diversity-stability relationship. He suggests that we need to understand the structural-functional design of communities, rather than be preoccupied with diversity.

An alternative to the concept that diversity begets stability is to view plant and animal communities as nonequilibrium systems which do not exhibit thermodynamic forms of stability, but do exhibit organization by virtue of fluctuations in mortality of individuals (Royce 1977, 1978; Connell 1978). Diversity of species, or any other variable of interest, is then viewed as a consequence of the dynamics of the individuals composing the community. It is unimportant, therefore, whether or not a community is stable, or whether differences in the number and distribution of species are related to a certain definition of stability. An unmanaged forest behaves as a nonequilibrium, aimless community that is the consequence of the behavior of individualistic systems (Boyce 1977, 1978).

An unmanaged forest has no centralized information network and a decision mechanism to direct the mortality and the behavior of individuals. Thus, there can be no goals such as achieving and maintaining a state of stability. If there were such a goal, evolution and extinction could not have occurred as indicated by the fossil and genetic evidence for billions of years (Simpson 1969; Dobzhansky and others 1977). Without a centralized information network, diversity of species is a consequence of the behavior of individualistic systems. Thus, we view unmanaged forests as aimless systems. People can develop information networks and easily become the centralized decision mechanism that converts these aimless communities to directed systems (Boyce, In press).

Algorithms, similar to the ones we described for deer habitat in section 2.2, can be developed to relate the elements of forest diversity to multiple-use objectives. Such algorithms can be developed for any benefit, desirable or undesirable, for any specific forest area. Different forest areas will require adjustments in the algorithms to reflect differences in climates, soils, and topography. In this way, decisions can be made to provide for the diversity of plant and animal communities to meet overall multiple-use objectives. These relationships are discussed in greater detail in section 5.

2.4 Confounding in the Shannon-Type of Diversity Indices

In this section we relate the Shannon function to a large number of similar mathematical functions. Procedures for calculation are described. We illustrate how these functions confound classes and proportions of things and, thus, cannot be used to develop relationships for use in management decisions. The Shannon function (Shannon and Weaver 1949) is frequently used to compute dimensionless numbers that express diversity (Pielou 1977; Hair, In press). Because of the widespread use of the Shannon and similar functions, it is important to explain the computation methods and the characteristics of these dimensionless numbers.

R. A. Fisher developed a function to describe the expected frequencies with which different species occur in random collection (Fisher, Corbet, and Williams 1943). Weiner (1948) and Shannon (Shannon and Weaver 1949) developed similar functions for measuring uncertainty in communication systems. Brillouin (1962, 1964) used a large number of modifications of the same basic function. Engen (1977) showed how many of these functions, including the Simpson index (Pielou 1977), could be derived from or related to the Shannon function. Tribus (1961) showed that the Shannon function is related to a measure of entropy and can be used in thermodynamics. However, as Hill (1973) pointed out, there is no particular biological significance in the origin of the Shannon and related functions. We describe the Shannon function, since it is frequently used and it is representative of the others.

Indices computed with the Shannon and related functions are dimensionless numbers that confound a number of classes of things and the proportion of things in each class. This confounding is desirable in thermodynamics (Tribus 1961) and in measuring uncertainty in communications. Pielou (1977, page 292) emphasizes the need to be aware of confounding when the Shannon function is used as an index for diversity. Because of confounding, the index cannot be used as an independent variable for some benefit such as the livelihood for deer (figs. 1, 2, and 3).

'The Shannon function can be computed any time a group of items can be placed in discrete classes and the proportions of items among classes can be measured. Examples of classes of things and proportions are the number of species and the proportion of individuals assigned to each species, forest types and the proportion of area assigned to each type, species of breeding birds and the proportion of birds in each species, tree species and the proportion of basal area by species, tree species and the proportion of individuals assigned to each species, and species of game animals and the proportion of animals in each species. Classes of things can be considered singly and in many possible combinations. Here we limit ourselves to no more than two classes of things occurring jointly.

Computation of the index is relatively simple. To illustrate the procedure, we use data from inventories of forests in the Mountain Region of North Carolina and of the Pisgah and Nantahala National Forests (Cost 1975). The National Forests are included in the Mountain Region, which consists of 21 western counties in North Carolina.

From the data (Cost 1975) we prepare a table of forest types and the proportion of area in each type for each of the forest areas (table 1). Computation begins by multiplying each proportion (p) by the natural logarithm of that value. For example, on the Pisgah National Forest the oak-hickory type occupies 74.5 percent of the area. The number, 0.745, is multiplied by the natural logarithm of 0.745, which is -0.2944. The product is -0.219. Since the logarithms of numbers less than 1 are negative, the product is multiplied by -1 to produce a positive value (table 1). Then, for each forest area the logarithmic proportions (plnp) are summed to produce the diversity index. The letter H' is used to symbolize diversity index because this is the symbol used in most of the biological literature. Natural Logarithms are used because of convention.

The Shannon function is usually written in the form:

$$H' = -K\sum_{i=1}^{n} pi \ln pi$$

Where K is a constant, usually -1, that amounts to converting H' to a positive value. Pi is the proportion of the ith class.

Table 1.--Computation of the Shannon diversity index for areas of forest types found on the Pisgah and the Nantahala National Forests and the Mountain Region Survey in North Carolina

Forest types	Pisgah National Forest		Nantahala National Forest		Mountain Region Survey	
	Percent	p·lnp[1]	Percent	p·lnp[1]	Percent	p·lnp[1]
White pine-hemlock	2.4	0.090			3.4	0.115
Spruce-fir	1.2	.053	--	--	0.3	.017
Loblolly pine	--	--	1.7	0.069	0.4	.022
Shortleaf pine	--	--	--	--	0.6	.031
Virginia pine	1.5	.063	--	--	5.3	.156
Pitch pine	7.1	.188	1.2	.053	1.4	.060
Oak-pine	4.8	.146	7.7	.198	8.7	.212
Oak-hickory	74.5	.219	63.4	.289	69.5	.253
Chestnut oak	5.7	.163	18.5	.312	4.5	.140
Elm-ash-cottonwood	--	--	--	--	0.2	.012
Maple-beech-birch	2.8	.100	7.5	.194	5.7	.163
Total	100.0		100.0		100.0	
H' = Total p·lnp		1.022		1.115		1.181

Forest areas

[1] The proportion of a type (p) multiplied by the natural logarithm of the same value (lnp).

The diversity indices (1.022, 1.115, 1.181) for the three forest areas are dimensionless values (table 1). The size of the values is determined by the number of forest types found on each forest area and by the proportion of land distributed among the forest types. These two quantities are confounded to form a single number. We illustrate this with a few computations.

The maximum possible value of the Shannon diversity index occurs when all forest types are evenly distributed. For example, if the land area of each forest was evenly distributed among the **11** types, the proportion of each type would be 1/11=0.09091. The natural logarithm for 0.09091 is -2.3979, which is multiplied by 0.09091 and **-1** to produce the positive value of 0.21799 for each type. This value is multiplied by 11, the number of types to produce the maximum value for H', which is 2.3979. By examining a table of natural logarithms, one can confirm that this value (2.3979) is the natural logarithm of 11. Thus, the maximum possible value for the Shannon index is the natural logarithm of the number of classes of the items.

The degree of evenness of the forest types can be assessed by dividing the diversity index (H') by the maximum possible value, which is the natural logarithm of the number of types. For the Region, the evenness is 1.181/2.3979=0.49; for the Pisgah the evenness value is 1.022/2.3979=0.43; and for the Nantahala the evenness value is 1.115/2.3979=0.46. Since maximum evenness occurs when the value is 1.0, the forest types recorded on the Nantahala are quantitatively illustrated to be less evenly distributed than in the Region but mare evenly distributed than on the Pisgah. The greater evenness of types for the Nantahala accounts for the larger diversity index than for the Pisgah, although the Pisgah has more kinds of forest types (table 1). The Shannon diversity indices are shown to confound the number of forest types (classes) and the proportions of area in each forest type (proportion of things in each class) to form the dimensionless numbers, H'.

The important point is that the Shannon-type indices give us very limited information about the diversity of types and other elements of communities. And the Shannon-type indices, because of confounding, cannot be used as independent variables to develop relationships for use in management decisions. We can, however, take advantage of the confounding effect of the functions to indicate how much specified elements of communities are constrained from evenness. This provides the basis for monitoring how the constraint of habitats may affect the livelihood of organisms. The method is described in the next section.

2.5' How to Monitor Constraint in the Distribution of Habitats

In this section we describe and illustrate how a modification of the Shannon-type function can be used to monitor how habitats may be constrained from an even distribution by alternative management plans. The significance of constraint in the distribution of habitats is that the livelihood may be limited for a number of endemic species. Constraint of habitats may be increased or decreased by management actions or by forces unaffected by man.

From section 2.4 evenness is H' divided by the logarithm of the number of habitats being considered. If we subtract the value for evenness from 1, we have a relative measure of constraint, which we call constraint quantum (CQ).

The equation can be expressed in the following form:

$$CQ = \frac{\left(\sum_{i=1} pi \cdot \ln pi \right) + \ln N}{\ln N}$$

Where pi is the proportion of the ith class of habitat, lnpi is the natural logarithm of the proportion of the ith class and lnN is the natural logarithm of the number of classes of habitats.

Shannon recognized this expression as a measure of constraint in languages, which he called redundancy. Ashby (1956) used the word "constraint," and described various uses for the expression. Our concern is to use CQ to monitor when the livelihood for some kinds of endemic organisms is being reduced.

For an illustration we use an inventory of seven kinds of habitats. Each habitat is defined by a stand condition class in a hardwood forest, 6,396 acres, in Buncombe County, North Carolina. Other classifications could be used; however, it is important that the classes meet the operational criteria for elements of diversity (sec. 2.1).

Seedling habitats.--Stands with half of the dominant and codominant trees less than 1 inch d.b.h. (2.5 cm). A few scattered large trees are admitted.

Sapling habitats.--Stands with half of the dominant and codominant trees between 1 and 5 inches d.b.h. (2.5 to 12.4 cm). A few scattered large trees are admitted.

Pole habitats..--Stands with half of the dominant and codominant trees between 6 and 11 inches d.b.h. (12.5 to 27.7 cm). Pole habitats are classified by 2-inch (5 cm) diameter classes as pole-6, pole-8, and pole-10 habitats.

Mature timber habits.--Stands with half of the dominant and codominant trees between 11 and 16 inches d.b.h. (27.8 to 40.6 cm).

Old-growth habitats.--Stands with half of the dominant and codominant trees larger than 16 inches d.b.h. (40.7 cm).

First we consider a mode of management when no timber is harvested and the forest changes with forces unaffected by man (fig. 4). A dynamic, analytic silviculture technique (Boyce 1977) is used to display changes over time. The proportion of old-growth habitat increases to about *63* percent of the area. The CQ value (*) remains below about *0.2* until year *30,* then the constraint quanta increase to about *0.34* by year 110. The increase in constraint results from an increase in the proportion of area in old-growth (O) and in the reduction of area in seedling (S), sapling (A), and pole-6 (6), pole-8 (8), and pole-10 (1) stands. The proportions of areas in the younger habitats are constrained by the large area in old growth. The increasing constraint in the distribution of habitats is monitored by the increase in constraint quanta.

Our concern is with changes in the proportional distribution of habitats, especially an increase in constraints that would limit the availability of one or more habitats. The significance of this information for wildlife is given by Siderits and Radtke (1977):

> "A wildlife plan or program then becomes the establishment of the desirable mixture of various coniponents that will provide the greatest diversity through time and space on a sustained basis. A management plan geared to provide this diversity would have as its goal not a given number of animals of any one species, but a given acreage of quality environment that would support a variety of species in different densities, dependent upon the inherent capability of the area being managed."

We now consider a mode of management (Boyce 1977) in which rates of timber harvest from the mature and old-growth stands and sizes of openings would increase the random proportions and locations of the seven habitats. The CQ values (fig. 5) decline for about 40 years and then remain at about 0.05. The value *0.05* simply indicates less constraint on the distribution of habitats than when the CQ values are larger, such as *0.34* (fig. 4). Relatively smaller CQ values indicate a relatively mare even distribution of habitats and the livelihood of a greater number of genotypes (sec. 2.2).

From Coyle's (In press) work with spiders, one would expect more different kinds of spiders to be found in the forest with a CQ value of *0.05* than in one with a CQ value of *0.34.* However, we do not have enough information to know what range of CQ values for this particular forest and for these seven classes of habitats would provide a livelihood for the largest numbers of endemic species. Relationships such as the algorithms for deer (figs. 1, 2, and 3) must be obtained for each kind of forest and for widely diverse kinds of plants and animals.

One could use a modification of the Shannon-type of functions as a relative measure of the constraint of habitats. None of the functions have any particular biological significance. Such functions are nothing more than a relative measure of constraint of habitats from evenness. What is important is that one specify the number and kinds of habitats and have evidence that diversity of the kinds of habitats described relate to the potential livelihood of most, if not all, endemic species. The significance of the constraint quantum lies in its use to indicate when one or more of these important kinds of habitats is being constrained beyond a desirable distribution.

PERCENT OF AREA BY HABITATS AND THE CONSTRAINT QUANTA VALUES

YEARS

```
     .0             .1             .2             .3             .4 S
     .0             .2             .4             .6             .8 A681MO*
    0- O MS- -8-*- -A- - -16 - - - - - - - - - - - - - - - - - - -
     . O SM    8    A     6                                      . 61,8*
     . OS  M   8    A    6                                       . 61,8*
     .  S   M * 8  A.    61                                      . SO
     . SO    M* 8  A.  6 1
     . SO    M*  8 A.  6 1
     .S O    *M  8 A. 6 1
     .S O    * M 8A .6  1
     .S  O   *  M A .6  1                                        . A8
     .S  O   *  M A 6   1                                        . A8
  10.-S- O - * - A86 - -1- - - - - - - - - - - - - - - - - - - - AM
     S     O* A68M.     1
     S      O  A6 8 .M 1                                         . O"
     S      * A  8  .  1                                         . A6O,1M
     S       A  8   .  1M                                        . A6*,8O
     .S     A* 8  O . 1   M                                      . A6
     .S    A  *8    O1    M                                      . A6
     .S   6A  8*    .1O    M
     .S   A     8   1   O   M                                    . A6
     .S   6A 8   * 1.     O M
  50.-S- 6A8 - - -1- - - - -MO - - - - - - - - - - - - - - - - - 1*
     .S  6A8     1 *.       M   O  .
     .S 6 A     1   *       M    O .                             . A8
     .S 6 A    1     *     M       O                             . A8
     . S68A    1    . *    M       .O
     . S68A   1     .  *  M        .  O
     . S68A  1      .   * M        O
     . S6 A  1           M               O                       . 68,M*
     . S6 A 1       .   M *                O                     . 68
     . S6 A1        .  M   *                O                    . 68
  90.- S6-A1 - - - - - M - * - - - - - - - - O - - - - - - - - - 68
     . S6 A1        . M     *                 O   .              . 68
     . S6 1A        .M       *                 O  .              . 68
     . 56 1A        M        *                  O .              . 68
     . 56 1A      M.         *                   O.              . 68
     . 56 1A      M.          *    .             O.              . 68
     . 561 A      M .         *    .              O              . 68
     . 561 A      M .         *    .              .O             . 68
     .  S1  A    M  .         *    .              .O             . 568
     .  S1  A   M   .          *   .              .O             . 568
 130.- -S1 -A- -M- - - - - - - * - - - - - - - - - O - - - - - - S68
     .  S1  A   M   .          *   .              . O            . S68
     .  S1  A  M    .          *   .              . O            . S68
     .  S1  A  M               *   .              . O            . 568
     .  S1  A  M               *   .              . O            . S68
     .  S1  A M                *   .              . O            . 568
     .  S1  A M                *   .              . O            . 568
     .  S6  A M               *    .              . O            . 58.61
     .  S6  A M               *    .              . O            . S8,61
     .  S6  A M               *    .              . O            . S8,61
 170.- -S6 - A - - - - - - - -*- - - - - - - - - - -O- - - - - - S8,61,AM
```

Figure 4.--When no timber is harvested, the proportion of old-growth habitat (O) increases and constrains the amount of mature timber (M), pole timber (1, 8, 6), saplings (A), and seedlings (S). This constraint is indicated by the rise in constraint quanta (*).

PERCENT OF AREA BY HABITATS AND THE CONSTRAINT QUANTA VALUES

YEARS

```
   .0             .1             .2             .3             .4 S
   .0             .2             .4             .6             .8 A681MO*
.0- O MS- -8-*- -A- - -16 - - - - - - - - - - - - - - - - - - - - - -
   . O SM     8     A     6                                    . 61,8*
   . OS  M    8     A     6                                    . 61,8*
   . OS   M * 8   A.    61
   . OS    M* 8   A.   6 1
   . OS    M*  8 A.   6 1
   . OS    *M  8 A. 6 1
   . O S   *M  8 A.6   1
   . O S  *  M  8A.6   1
   . O S  *  M  8A6    1
10.- O S -*- -M-8A - -1- - - - - - - - - - - - - - - - - - - - - A6
   .  O S*     M6A.   1                                        . 68
   .  O S*    68A.   1                                         . 8M
   .   OS    6 8 A .  1                                        . AM,S*
   .   OS   6  8 AM  1                                         . S*
        S   6 8  A.M1                                          . SO*
        SO  6 8   AM1                                          . S*
   .   * SO6 8    A1                                           . 1M
   .   * SO6 8    A1M
   .   * S 68     A M                                          . A1,6O
50.- - * S 68- - -1AM- - - - - - - - - - - - - - - - - - - - - - 8O
   .   * S 68    I.A                                           . AM,8O
   .   * S 68O   I.A                                           . AM
       * S 6 O  1 .MA                                          . 68
   .  *  S 6 O  1 .MA                                          . 68
   .  *  S 6  O 1 M A                                          . 68
   .  *  S 6  O1  M A                                          . 68
   .  *  S 6  O1 M.  A                                         . 68
   .  *  S 86 O1 M.  A
   .  *  S 86 O1 M.  A
90.- -*- -S86- 1M- - A - - - - - - - - - - - - - - - - - - - - - 1O
   .  *   S 6  1M .  A                                         . 68,1O
   .  *   S 6  1M .   A                                        . 68,1O
   .  *   S 6  1  .   A                                        . 68,1MO
   .  *   S 6  1  .   A                                        . 68,1MO
   .  *   S 6 O1  .   A                                        . 68,1M
   .  *   S 6 O1  .   A                                        . 68,1M
   .  *  S  6 0 1 .   A                                        . 68,1M
   .  *  S  6 0 1 .   A                                        . 68,1M
   .  *  S  6 M1  .   A                                        . 68,MO
130.- -*- S -6-M1 - - -A- - - - - - - - - - - - - - - - - - - - - 68 MO
   .  *  S  6 M1  .   A                                        . 68,MO
   .  *  S  86M1  .   A                                        . MO
   .  *  S  86M1  .   A                                        . 6O
   .  *  S  86M1  .   A                                        . 6O
   .  *  S  86M1  .   A                                        . 6O
   .  *  S  86M1  .   A                                        . 6O
   .  *  S   6M1  .   A                                        . 68O
   .  *  S   6M1  .   A                                        . 68O
   .  *  S   6M 1 .   A                                        . 68O
170.- -*- S -O6 M1- - -A- - - - - - - - - - - - - - - - - - - - - 68
```

Figure 5.--The constraint quanta of about 0.05 for habitats in this particular forest results in a certain combination of benefits being available at a relatively high rate. **S** = seedling habitat; **A** = sapling habitat; 6 = pole-6 habitat; 8 = pole-8 habitat; **1** = pole-10 habitat; M = mature timber habitat; O = old-growth habitat.

3. HOW TO COMPARE THE DIVERSITY OF TREE SPECIES

3.1 Direct Comparisons

Lists of species by some meaningful characteristic provide thr simplest way to compare diversity of tree species in the National Forests and in the Region (Oosting 1956; Harper 1977; May 1976). One of the most meaningful methods is to use a matrix for the proportions of species by size classes. This method provides a list of the most obvious species, information about the distribution of species by size classes, and data that may be used in logarithmic, bionomic, and geometric transformations (Pielou 1977). We illustrate this method.

From the inventory data ior the Mountain Region Survey in North Carolina (Cost 1975), we prepare three matrices of the proportions of trees in 32 species and species groups and in 12 diameter classes (tables 2, 3, and 4). Each number in the matrix is the percent of total individuals recorded and represents a unit of diversity of species and size classes. The nomenclature of the classes of species is listed in the Forest Survey Handbook (U.S. Dep. Agric., Forest Service 1967). Individuals are recorded regardless of their position in the stand and regardless of the condition class of the stand. Species are grouped into classes, either because of the difficulty of identifying individuals in all stages of development, or because the individuals represent less than 0.01 percent of the total.

Two-inch diameter classes are used to classify all stems from **1** to 20.9 inches d.b.h. (tables 2, 3, and 4). Because of the low frequency of trees larger than 20 inches, one class includes trees From 21.0 to 28.9 inches and a last class includes all trees larger than 29 inches d.b.h. 'The diversity of diameter classes is illustrated with logarithmic paper (fig. 6). These kinds of curves have been known for many years (Husch and others 1972). Certain kinds of management actions, especially those that limit the presence of stands in certain diamrter classes, can change the elevation, shape, and slope of these curves (Assmann 1970; Smith 1962). For example, the higher elevation of the curve for the Pisgah National Forest indicates a larger average diameter ior trees in the Pisgah than in the Nantahala and in the Region.

The logarithmic relationships can be used to examine the relative diversity of species by diameter classes. Stands, whether of mixed species or of a single species, are organized over time by the mortality of individualistic systems (Boyce 1977, In press). Different genotypes form with the environment different individualistic systems, each having a difierent probability that the essential variables, such as water content, and respiration rates, can be maintained within the limits of life. Thus, we would expect, and we find, different natural rates of mortality among genotypes and thus, species. The significance of these natural, biological mechanisms is to change the diversity of species as groups of stands change to larger diameter classes.

For example, we find a greater diversity of tree species in the smaller diameter classes, typical of seedling and sapling habitats, than in the larger diameter classes, typical of mature and old-growth habitats (for definitions of the classes of habitats, see section 2.5). We illustrate this relationship with a limited number of examples.

Table 2.--Relative numbers of tree species for diameter classes for the Mountain Region Survey in North Carolina

Tree species	Diameter class												
	1.0-2.9	3.0-4.9	5.0-6.9	7.0-8.9	9.0-10.9	11.0-12.9	13.0-14.9	15.0-16.9	17.0-18.9	19.0-20.9	21.0-28.9	29.0 and larger	Total
	percent												
Shortleaf pine	0.40	0.21	0.14	0.18	0.14	0.07	0.04	(1/)	(1/)	(1/)	(1/)	--	1.18
Loblolly pine	.08	.09	.03	.04	.01	--	--	--	--	--	--	--	.25
Virginia pine	2.30	1.05	.82	.48	.25	.08	.03	0.01	(1/)	(1/)	--	--	5.02
Pitch pine	.38	.39	.29	.22	.15	.06	.03	.02	0.01	(1/)	(1/)	--	1.55
Table-Mountain pine	.04	--	.03	.03	(1/)	.01	.01	(1/)	--	--	(1/)	--	.12
Eastern white pine	1.99	.56	.21	.27	.15	.09	.07	.05	.03	0.01	0.02	(1/)	3.45
Eastern hemlock	.80	.28	.21	.07	.05	.02	.03	.02	.01	.01	.01	(1/)	1.51
Spruce and fir	.39	.08	.02	.04	.02	.01	(1/)	(1/)	(1/)	--	--	--	.56
Cedars	.07	.10	.02	(1/)	(1/)	--	--	--	--	--	--	--	.19
Select white oaks	2.19	1.03	.43	.24	.15	.11	.06	.03	.04	.02	.02	(1/)	4.32
Select red oaks	.85	.68	.31	.20	.14	.12	.08	.06	.04	.03	.04	0.01	2.56
Chestnut oak	1.88	1.18	.68	.46	.32	.20	.15	.10	.05	.04	.05	.01	5.12
Other white oak	.22	.03	.04	.01	.02	.01	(1/)	(1/)	--	--	--	(1/)	.33
Other red oak	1.86	1.24	.78	.50	.36	.22	.15	.09	.05	.03	.03	(1/)	5.31
Hickory	2.56	.87	.37	.24	.17	.11	.07	.04	.03	.01	.01	(1/)	4.48
Yellow birch	.19	.23	.16	.02	.02	(1/)	.01	.01	(1/)	(1/)	(1/)	(1/)	.64
Hard maple	.71	.2h	.14	.05	.02	.02	.02	.01	.01	(1/)	(1/)	(1/)	1.24
Soft maple	8.07	2.37	.93	.37	.21	.12	.07	.04	.02	.01	.01	(1/)	12.22
Beech	1.54	.32	.19	.07	.05	.04	.03	.01	.01	(1/)	.01	--	2.27
Sweetgum	--	.03	.01	.01	(1/)	(1/)	--	(1/)	--	--	--	--	.05
Tupelo and blackgum	3.36	.47	.1h	.07	.04	.04	.02	.01	.01	(1/)	(1/)	--	4.18
Ash	.25	.07	.09	.07	.02	.03	.02	.01	.01	(1/)	(1/)	(1/)	.57
Cottonwood	--	--	--	--	--	--	--	--	--	--	(1/)	--	(1/)
Basswood	.31	.14	.05	.05	.03	.03	.01	.01	(1/)	(1/)	(1/)	(1/)	.63
Yellow-poplar	3.04	1.41	.70	.52	.36	.26	.16	.08	.04	.02	.02	(1/)	6.61
Bay and magnolia	.29	.16	.03	.04	.02	.01	.01	.01	(1/)	(1/)	(1/)	(1/)	.57
Black cherry	.45	.05	.07	.03	.02	.01	.01	(1/)	(1/)	(1/)	(1/)	--	.64
Black walnut	.07	.05	.02	.03	.01	.01	(1/)	(1/)	(1/)	(1/)	(1/)	--	.19
Sycamore	--	--	--	--	.01	--	--	--	--	--	--	--	.01
Black locust	.81	.38	.33	.30	.18	.11	.05	.02	.01	(1/)	.01	--	2.20
Elm	.05	--	--	--	--	--	--	--	(1/)	--	--	--	.05
Other eastern hardwoods	22.36	6.46	1.93	.70	.28	.12	.06	.03	.02	.01	.01	(1/)	31.98
Total	57.51	20.19	9.19	5.31	3.20	1.91	1.19	.66	.39	.19	.24	.02	100.00

1/ Less than 0.01 percent.

Table 3.--Relative numbers of tree species for diameter classes for the Pisgah National Forest

Tree species	Diameter class												
	1.0-2.9	3.0-4.9	5.0-6.9	7.0-8.9	9.0-10.9	11.0-12.9	13.0-14.9	15.0-16.9	17.0-18.9	19.0-20.9	21.0-28.9	29.0 and larger	Total
	- - - - - - - - - -			- -	- - - - - - - Percent			- - - - - - - - - - - -					- -
Shortleaf pine	--	--	0.15	0.17	0.16	0.07	0.04	--	--	--	--	--	0.59
Loblolly pine	--	--	--	--	--	--	--	--	--	--	--	--	--
Virginia pine	0.32	0.32	.20	.24	.08	.01	.02	--	--	--	--	--	1.22
Pitch pine	.03	2.43	.90	1.15	.44	.20	.04	0.05	0.02	0.01	--	--	5.53
Table-Mountain pine	--	--	.10	.24	--	.09	.04	.02	--	--	--	--	.49
Eastern white pine	.33	.32	.33	.51	.22	.14	.01	.01	.03	.01	0.07	0.01	2.02
Eastern hemlock	1.23	--	.94	.20	.04	.08	.10	.05	--	.01	.03	.02	2.16
Spruce and fir	--	--	--	.15	--	--	--	--	--	--	--	--	.15
Cedars	--	--	--	--	--	--	--	--	--	--	--	--	--
Select white oaks	.32	.28	.75	--	.04	.05	--	.05	.05	.05	.05	(1/)	1.63
Select red oaks	1.21	1.50	.39	.31	.18	.33	.18	.17	.05	.16	.16	.05	4.75
Chestnut oak	2.10	.03	1.55	.86	.47	.35	.21	.14	.11	.10	.13	.03	6.35
Other white oak	--	--	--	--	--	--	--	--	--	--	--	--	--
Other red oak	.87	--	1.39	.81	.40	.24	.10	.14	.05	.07	.02	.01	3.97
Hickory	4.03	.64	.16	.02	.34	.01	.06	.05	.02	.02	.04	--	5.74
Yellow birch	.28	--	.08	.18	.11	.02	.01	.05	--	.01	.02	--	.82
Hard maple	.28	--	.28	.15	--	.04	--	--	--	(1/)	(1/)	.01	.75
Soft maple	10.87	3.63	1.55	.49	.42	.19	.15	.04	.05	.01	.02	.01	17.43
Beech	.30	.88	.21	--	.13	.03	.04	.03	.07	--	.02	--	1.68
Sweetgum	--	--	--	--	--	--	--	--	--	--	--	--	--
Tupelo and blackgum	4.84	--	.35	.15	--	.08	.02	.03	.02	.01	.01	--	5.51
Ash	--	--	.15	--	--	.01	--	--	--	--	--	--	.18
Cottonwood	--	--	--		--	--	--	--	--	--	--	--	--
Basswood	--	--	--	.03	.02	.05	.01	--	--	.01	--	--	.12
Yellow-poplar	.60	1.74	.43	.50	.19	.46	.22	.11	.09	.05	.05	--	4.64
Bay and magnolia	--	--	--	--	--	--	--	--	--	--	--	--	--
Black cherry	.28	--	.05	--	.02	.06	.01	.02	--	(1/)	--	--	.44
Black walnut	--	--	--	--	--	--	--	--	--	--	--	--	--
Sycamore	--	--	--	--	--	--	--	--	--	--	--	--	--
Black locust	.33	.65	.38	.14	.05	.23	.09	.06	--	--	--	--	1.93
mix	--	--	--	--	--	--	--	--	--	--	--	--	--
Other eastern hardwoods	18.97	9.12	2.74	I	.55	.30	.09	.09	.01	.04	.01	--	31.30
Total	45.30	21.80	13.08	8.21	4.05	3.04	1.49	1.17	.75	.58	.60	.14	100.00

1/ Less than 0.01 percent.

Table 4.--Relative numbers of tree species for diameter classes for the Nantahala National Forest

Tree species	Diameter class												
	1.0- 2.9	3.0- 4.9	5.0- 6.9	7.0- 8.9	9.0- 10.9	11.0- 12.9	13.0- 14.9	15.0- 16.9	17.0- 18.9	19.0- 20.9	21.0- 28.9	29.0 and larger	Total
	Percent												
Shortleaf pine	--	--	--	0.11	0.23	0.09	0.07	0.01	--	0.01	--	--	0.52
Loblolly pine	--	0.62	0.30	.38	.05	--	--	--	--	--	--	--	1.35
Virginia pine	--	.21	.06	.12	.05	.01	--	--	--	--	--	--	.45
Pitch pine	1.15	1.38	.19	.33	.10	.04	.04	.01	0.01	--	--		3.27
Table-Mountain pine	--	--	.07	--	--	--	.02	--	--	--	0.01	--	.10
Eastern white pine	0.46	.40	.04	.27	.10	.05	.05	.04	--	.01	.04	0.01	1.47
Eastern hemlock	1.32	.46	.28	.13	.06	.01	.06	.03	.01	.02	.02	.02	2.42
Spruce and [illegible]	--	--	--	--	--	--	--	--	--	--	--	--	--
Cedars	--	--	--	--	--	--	--	--	--	--	--	--	--
Select white oaks	2.02	1.55	.51	.31	.16	.11	.04	.02	.10	.02	.06	--	4.90
Select red oaks	1.53	2.42	.73	.30	.32	.18	.08	.05	.04	.03	.09	.02	5.79
Chestnut oak	3.27	3.10	.70	.41	.41	.14	.17	.17	.05	.07	.13	.02	8.64
Other white oak	--	--	--	--	--	.02	--	.01	--	--	--	--	.03
Other red oak	1.45	1.72	.80	.63	.57	.40	.38	.13	.10	.05	.07	.01	6.31
Hickory	5.38	2.83	.83	.37	.20	.22	.17	.06	.06	.01	.02	(1/)	10.15
Yellow birch	.63	--	.12	--	.01	--	.02	.01	.01	.01	.01	.01	.85
Hard maple	.20	--	--	--	--	--	--	.01	--	--	.01	--	.22
Soft maple	10.38	3.99	1.23	.54	.21	.13	.04	.06	.02	--	.02	--	16.62
[illegible]	2.78	.20	.20	.05	--	.04	.11	.02	.01	.01	.01	--	3.43
Sweetgum	--	--	--	--	--	--	--	--	--	--	--	--	--
Tupelo and blackgum	2.42	.40	--	.10	--	.01	--	--	--	--	--	--	2.95
Ash	--	--	.21	.05	--	.04	.02	--	.02	--	--	--	.34
Cottonwood	--	--	--	--	--	--	--	--	--	--	--	--	--
Basswood	.23	.69	--	--	--	.07	.03	.03	--	--	.01	--	1.06
Yellow-poplar	1.38	.43	.28	.35	.18	.10	.07	.04	--	.02	.02	(1/)	2.87
[illegible] and magnolia	--	--	--	--	--	--	--	--	--	--	--	--	--
Black cherry	.46	--	--	--	.01	--	.03	--	--	--	--	--	.52
[illegible] walnut	--	--	--	--	--	--	--	--	--	--	--	--	--
Sycamore	--	--	--	--	--	--	--	--	--	--	--	--	--
[illegible]	.46	.44	--	.05	.13	.04	--	.01	.04	--	--	--	1.17
Elm	--	--	--	--	--	--	--	--	--	--	--	--	--
Other eastern hardwoods	13.77	7.31	2.01	.82	.33	.13	.11	.03	.03	.01	.02	(1/)	24.57
Total	49.29	28.15	8.56	5.32	3.16	1.85	1.51	.76	.50	.27	.54	.09	100.00

[1/] Less than 0.01 percent.

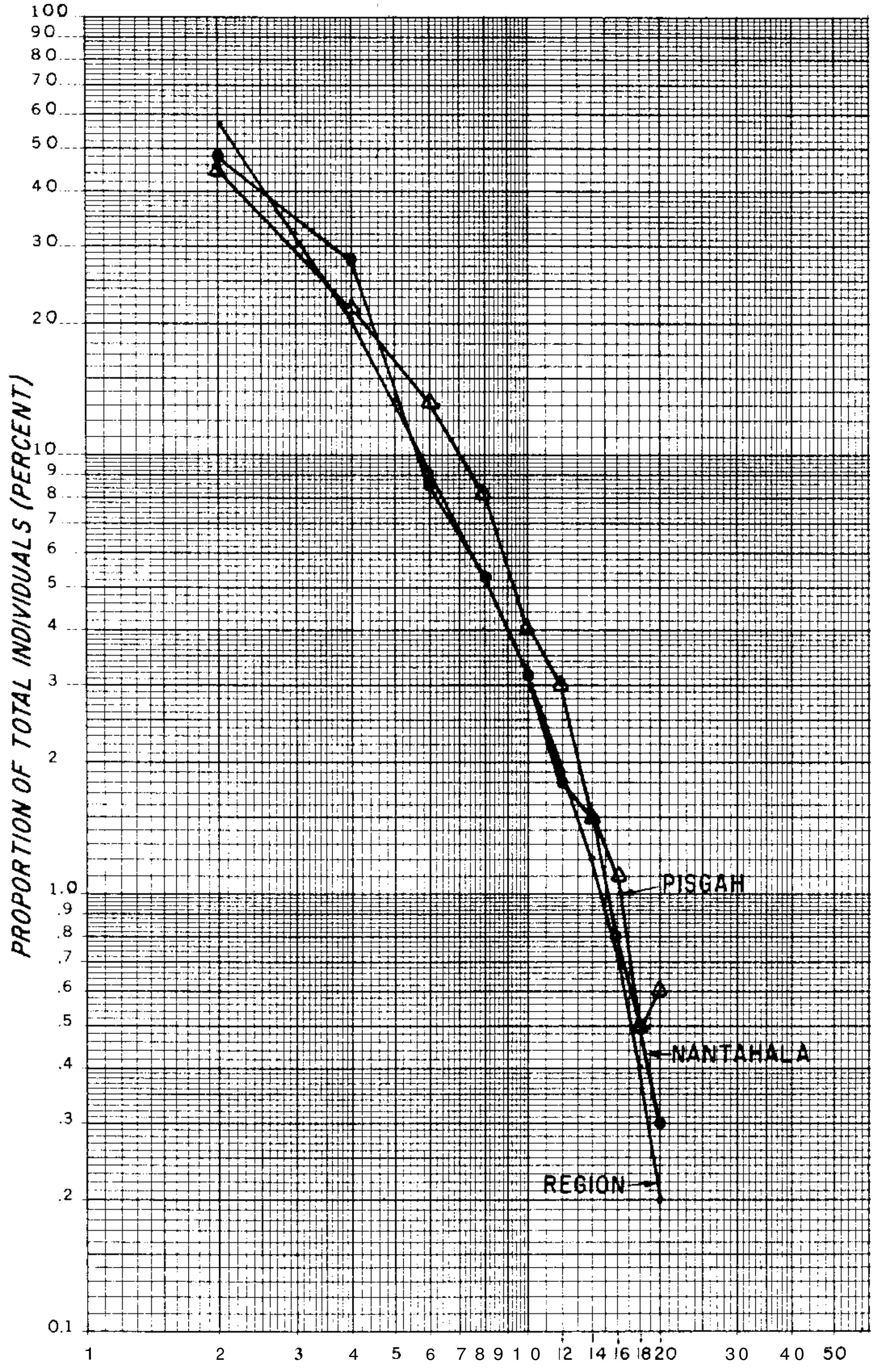

Figure 6.--The distribution of diameter classes for all species in the Mountain Region Survey and in the Pisgah and Nantahala National Forests.

The relatively infrequent species, labeled "other eastern hardwoods," such as dogwood and sourwood, represents 25 to 32 percent of the total individuals and 28 to 29 percent of the stems less than 5 inches d.b.h. (tables 2, 3, and 4). This kind of distribution is the common case for biological communities (Fisher, Corbet, and Williams 1943; Pielou 1977). Distributions are not random but are often logarithmic or follow some geometric form. Some of these species achieve large sizes, but most of them rarely become dominant and codominant trees. We can compute the proportions of these and other species by diameter classes by dividing each percentage figure by the total for the diameter class. For example, in the 2-inch-diameter class for the Region, the other eastern hardwoods represent 22.36/57.51=38.8 percent of the stems recorded.

We plot the percentages by diameter classes on logarithmic graph paper (fig. 7). The proportions of these infrequent hardwoods rapidly decline as the diameters increase above 4 inches. This is a consequence of relatively high rates of mortality as these species increase in diameter. From the graph (fig. 7), one can observe no outstanding differences between the Region and the National Forests.

Next to the infrequent hardwood species, soft maple has the highest percentage of any of the other species or species groups recorded (tables 2, 3, and 4). Soft maple represents 12 to 17 percent of all the numbers of stems recorded. However, 8 to 11 percent of these soft maple stems are less than 3 inches in diameter. Soft maple represents one of a number of species that has very high rates of mortality in the smaller diameter classes. This can be observed by plotting the proportions of soft maple by diameter classes on logarithmic graph paper (fig. 8). The rates of mortality for soft maple are not outstandingly different between the National Forests and the Region. The proportion of soft maple rapidly declines as diameter increases.

As a genus, the oaks represent a slightly larger proportion of total stems (17 to 26 percent) than soft maple. In contrast to soft maple, the oaks represent a group of species in which rates of mortality are relatively low, and consequently the proportion of oaks increases with increasing diameter class (fig. 9). The oak genus makes up more than half of all the trees larger than 16 inches in diameter. And the oaks are the most common dominant and codominant trees on both the Region and on the National Forests.

Large numbers of other hardwood and coniferous species have different rates of mortality with increasing diameter classes. These differential rates of mortality result in different combinations of species occupying dominant and codominant positions as stands age from seedling to old-growth habitats. Because of these changes, the distribution of species in seedling habitats is not directly related to the distribution of dominant and codominant species in mature and old-growth habitats. Some of these kinds of changes which result from different rates of mortality of species over time can be observed in the data reported by Della-Bianca (1971, 1975); Lamson and Smith (1978); Sander, Johnson, and Watt (1976); and Smith and Lamson (1977). Thus, interpretations of the diversity of species should consider differential rates of mortality, and the variety of stand condition classes.

Comparisons should consider, also, characteristics of indigenous soils. For example, pitch pine is more abundant in the National Forests than in the Region (tables 2, 3, and 4). The interpretation is that pitch pine naturally regenerates and survives to maturity on certain kinds of dry ridges. The kinds of ridges are more abundant on the National Forests, especially on the Pisgah, than on the Region. Thus, the differences in pitch pine are interpreted to be due to differences in indigenous soils.

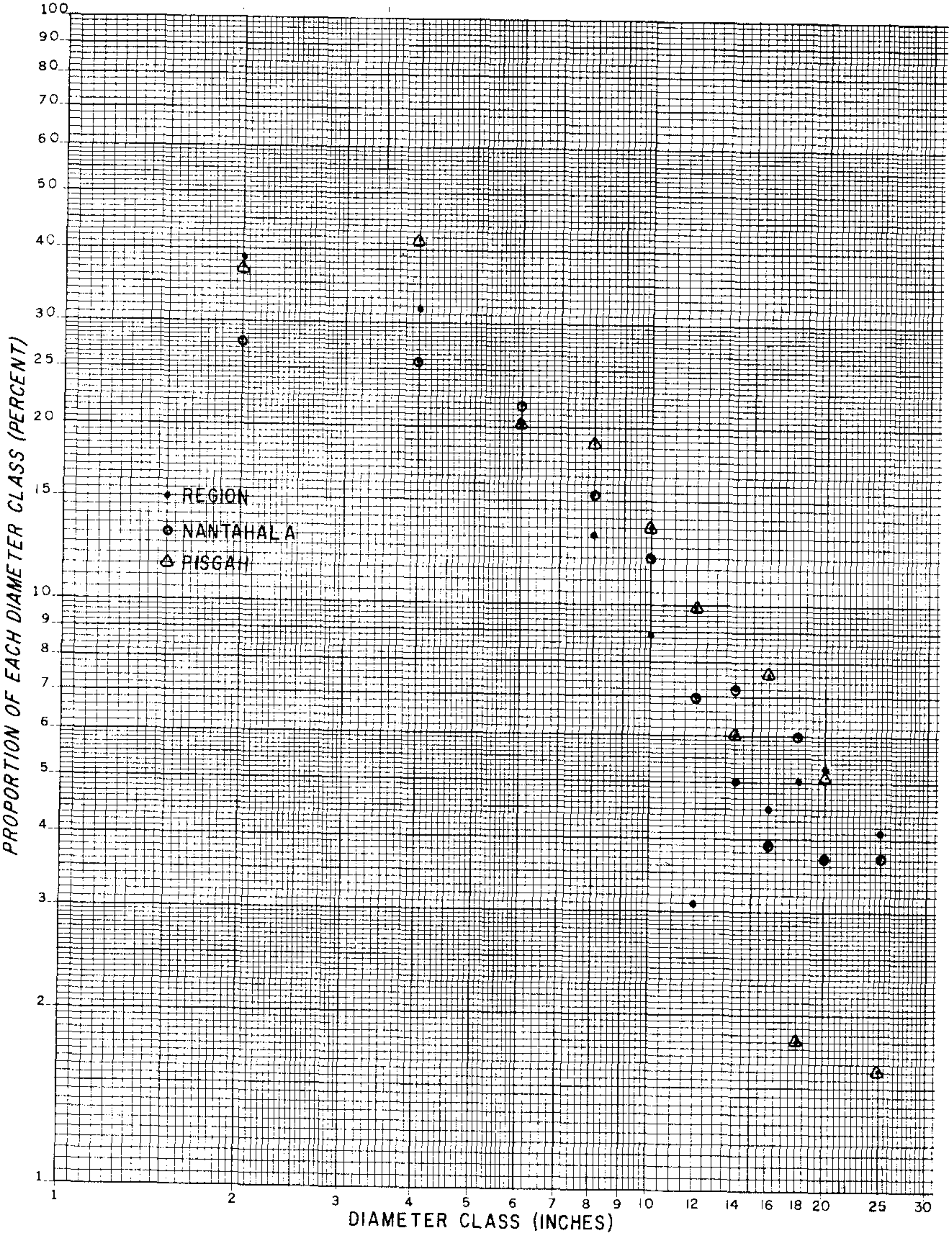

Figure 7.- h he proportion of each diameter class represented by "other hardwood species" (• = Mountain Region Survey; △ = Pisgah; and o = Nantahala National Forest).

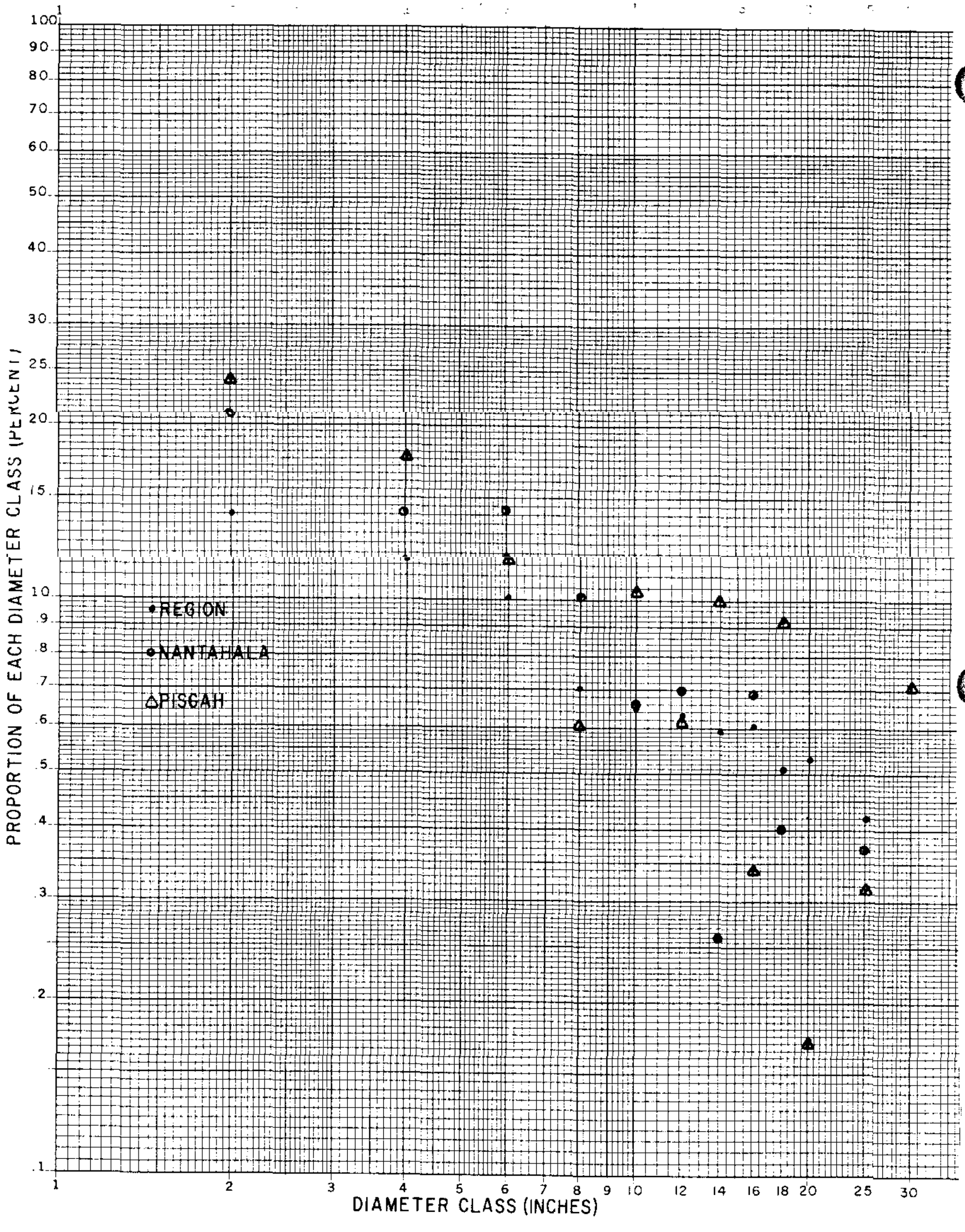

Figure 8.--The proportion of each diameter class represented by soft maple (• = Mountain Region Survey; △ = Pisgah; and o = Nantahala National Forest).

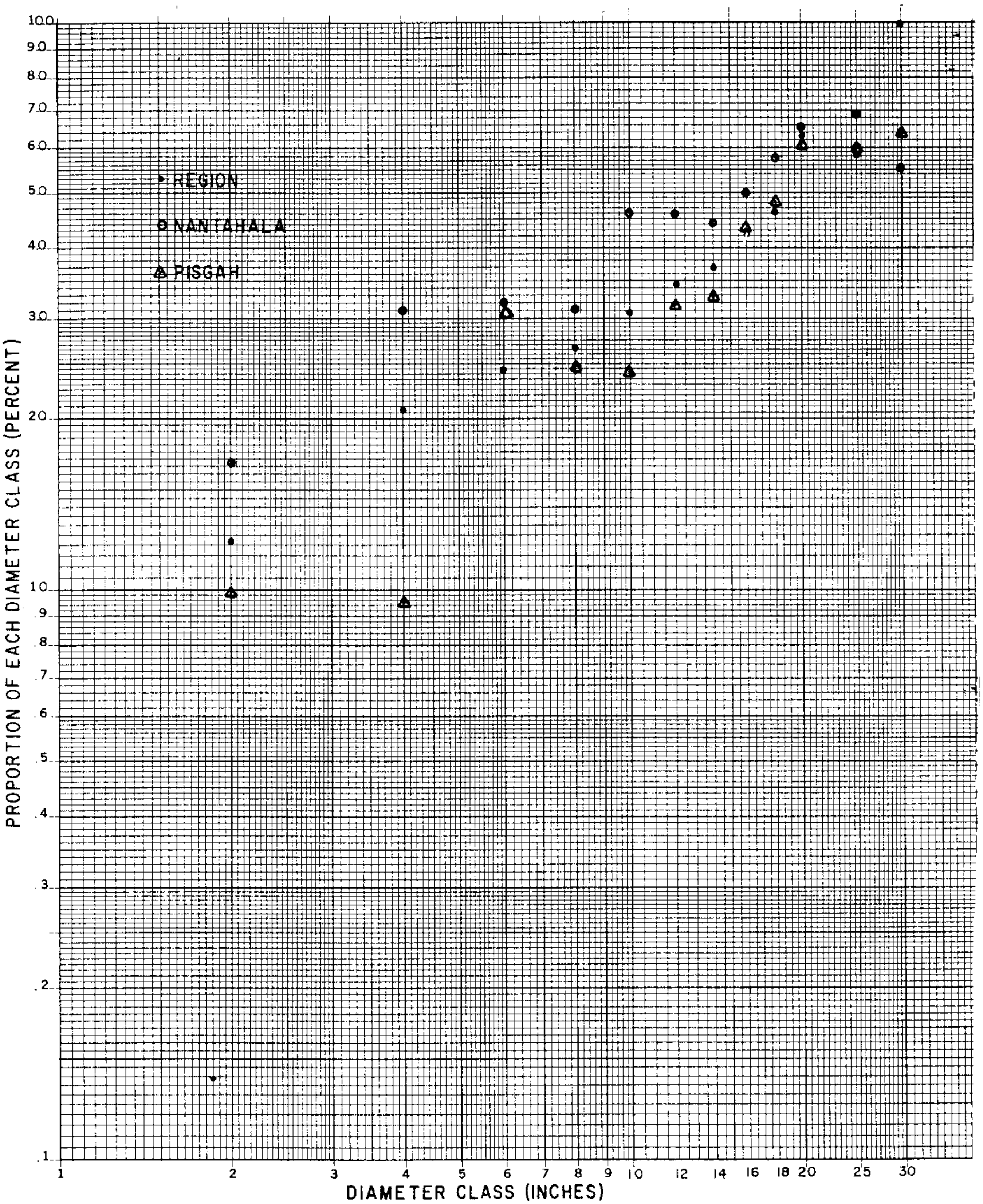

Figure 9.--The proportion of each diameter class represented by oaks (• = Mountain Region Survey; Δ = Pisgah; and o = Nantahala National Forest).

Our conclusion is that a direct comparison of the proportions of species by diameter classes is an effective way to compare the diversity of tree species in the Region and in the National Forests. It is important to use larger areas of land which provide a representative sample of diameter classes and species. Similarities and differences may be illustrated by logarithmic transformations of the data.

3.2 Indirect Comparisons with the Shannon Function

Because of the widespread use of the Shannon function for species diversity, we illustrate its use and its deficiencies. We find the Shannon function provides inadequate information.

For each of the three matrices (tables 2, 3, and 4), the joint diversity of species and diameter classes, H'(S,DC), the diversity for species, H'(S), and the diversity for diameter classes, H'(DC), were compueed by the methods illustrated in section 2.4 (table 1). For example, in the Mountain Region Survey, 8.07 percent of the soft maples is less than 3 inches d.b.h. (table 2). The natural logarithm of this value is multiplied by itself to Eorm the logarithmic proportions. These values are summed to form the joint diversity index. $H'(S,DC)=3.8036$ (table 2). The totals for rows are used for species (S) and the totals for columns are used for diameter classes (DC). The same computations are made for the two National Forests (tables 3 and 4). Evenness is computed as described in section 2.4. Values for the Shannon index and for evenness are listed for the three forest areas (table 5). The numbers are dimensionless and confounded (sec. 2.4).

Table 5.--The Shannon diversity and evenness indices for tree species, diameter classes, and the joint events for the Mountain Region Survey, the Pisgah and the Nantahala National Forests

Category	Mountain Region Survey	Pisgah National Forest	Nantahala National Forest
		Dimensionless	
Diversity			
Species	2.54	2.37	2.48
Diameter class	1.34	1.61	1.43
Joint event	3.80	3.74	3.78
Evenness			
Species	.73	.68	.71
Diameter class	.54	.65	.58
Joint event	.64	.63	.63

One can spend considerable time attempting to attach some kind of meaningfulness to the Shannon numbers (table 5). These kinds of numbers provide inadequate information for a rational interpretation of diversity in species and diameter classes, as described in section 3.1. We do not recommend the use of Shannon-type functions for comparing the diversities of tree species.

4. HOW TO COMPARE THE DIVERSITY OF COMMUNITIES AND ANTICIPATE CHANGES

4.1 Diversity of Communities

In this section we use lists of forest types by stand condition classes to illustrate a simple way to compare the diversity of plant and animal communities. A matrix of forest types by stand condition classes is prepared (tables 6, 7, and 8). Data are from Cost (1975). Each cell in the matrix is operationally defined as an element of diversity (sec. 2.1).

The oak-hickory type represents two-thirds to three-fourths of all the stands. And, most of the aak-hickory stands (39 to 50 percent) are in the sawtimber and old-growth condition classes. The chestnut oak type, 18 percent of the Nantahala, is an important type. Maple-beech-birch, pitch pine, and Virginia pine types each represent less than 10 percent of the forests.

Some of the differences (tables 6, 7, and 8) include: 30 kinds of different units of diversity recorded in the Region, 14 in the Pisgah, and 12 in the Nantahala; a greater proportion of sawtimber stands is recorded on both National Forests than in the Region; and the Pisgah has the highest proportion of nonstocked stands. These differences can he related to climate, soil types, and kinds of topography. For example, the nonstocked areas on the Pisgah are relatively steep areas with rocky soils. Nonstocked means the areas do not have a minimum number of commercial species of trees (Cost 1975). These areas do have an abundance of other kinds of plants and do contribute to the diversity of plant and animal communities.

An analysis of the reasons for the differences among the National Forests and the Region could provide important information for ways to maintain the current diversity of types and condition classes. Repeated inventories over time can provide data for future comparisons of forest types by stand condition classes (tables 6, 7, and 8) and for detecting major changes. One could use additional elements of diversity, such as the average area of stands. 'The elements used, however, should be meaningful, definitive, and measurable (sec. 2.1).

Comparisons such as this are useful primarily for monitoring changes in major elements of diversity over time. A more important consideration is how to anticipate change.

4.2 How to Anticipate Changes in the Diversity of Communities

In this section we use a dynamic analytic silviculture technique (Boyce 1977, 1978) to illustrate a way to anticipate changes in plant and animal communities. We show how one can anticipate changes in the diversity of communities under natural forces unaffected by man and under forces directed by man.

For the illustration we use an inventory of a hardwood forest, 6,396 acres, in Buncombe County, North Carolina. Each of seven stand condition classes is defined as a habitat (sec. 2.5). We use one forest type, oak-hickory. In practice more than one forest type may be used and habitats would then be defined as one of a number of stand condition classes in one of a number of forest types.

Table 6.--Diversity of forest types by condition classes of stands for the Mountain Region Survey in North Carolina

Forest types	Condition classes of stands				
	Sawtimber and old growth	Pole-timber	Saplings-seedlings	Nonstocked	Total
	- - - - - - - - -	Percent[1]	- - - - - - - - -		
White pine-hemlock	1.9	1.0	0.6	--	3.5
Spruce-fir	.2	--	--	0.1	.3
Loblolly pine	--	.2	.2	--	.4
Shortleaf pine	.3	.3	--	--	.6
Virginia pine	1.0	2.9	1.4	--	5.3
Pitch pine	.1	1.3	--	--	1.4
Oak-pine	3.3	4.3	1.0	--	8.6
Oak-hickory	38.9	24.2	5.9	.6	69.6
Chestnut oak	3.3	.6	.3	.2	4.4
Elm-ash-cottonwood	--	.2	--	--	.2
Maple-beech-birch	3.9	1.2	.2	.4	5.7
Total	52.9	36.2	9.6	1.3	100.0

[1] Percent of area.

Table 7.--Diversity of forest types by condition classes of stands for the Pisgah National Forest in North Carolina

Forest types	Condition classes of stands				
	Sawtimber and old growth	Pole-timber	Saplings-seedlings	Nonstocked	Total
	- - - - - - - - -	Percent[1]	- - - - - - - - -		
White pine-hemlock	1.2	1.2	--	--	2.4
Spruce-fir	--	--	--	1.2	1.2
Loblolly pine	--	--	--	--	--
Shortleaf pine	--	--	--	--	--
Virginia pine	--	1.5	--	--	1.5
Pitch pine	1.1	6.0	--	--	7.1
Oak-pine	4.8	--	--	--	4.8
Oak-hickory	50.1	20.3	2.6	1.5	74.5
Chestnut oak	4.1	1.6	--	--	5.7
Elm-ash-cottonwood	--	--	--	--	--
Maple-beech-birch	2.8	--	--	--	2.8
Total	64.1	30.6	2.6	2.7	100.0

[1] Percent of area.

Table 8.--Diversity of forest types by condition classes of stands for the Nantahala National Forest in North Carolina

Forest types	Condition classes of stands				
	Sawtimber and old growth	Pole- timber	Saplings- seedlings	Nonstocked	Total
	Percent[1/]				
White pine-hemlock	--	--	--	--	--
Spruce-fir	--	--	--	--	--
Loblolly pine	--	1.7	--	--	1.7
Shortleaf pine	--	--	--	--	--
Virginia pine	--	--	--	--	--
Pitch pine	--	1.2	--	--	1.2
Oak-pine	5.1	--	2.5	--	7.6
Oak-hickory	43.6	15.7	4.1	--	63.4
Chestnut oak	12.4	2.9	3.2	--	18.5
Elm-ash-cottonwood	--	--	--	--	--
Maple-beech-birch	6.1	1.5	--	--	7.6
Total	67.2	23.0	9.8	--	100.0

[1/] Percent of area.

Each habitat, a stand condition class of a forest type, is characterized by a definitive assembly of plants and animals. Habitats are constantly changing over time; birds, mammals, reptiles, and insects come and go; temperature, nutrient and water flows, and sediment movement vary continually; the flowering and growth of plants change seasonally and annually; and the rates of mortality of plants change as the community changes (sec. 3.1). We cannot anticipate very accurately all the kinds of species and the proportions of species plants and animals in a future community. We can anticipate, with an acceptable probability, that most naturally established forest types will remain in that forest type for some relatively long period of time. Over time, predictable changes will occur in most of the stand condition classes. But, unpredictable changes will occur in the proportions of most plants and animals. The kinds of dominant and codominant trees may he predicted with an acceptable probability. Thus, the most reliable basis for anticipating change is the physical changes in stand condition classes for a given forest type. For example, one can anticipate that a seedling habitat of a fdrest type will change to a sapling habitat of the same forest type during a predictable time. Figures 4 and 5 display these kinds of anticipated changes in the diversity of communities.

In section 2.5 we used the dynamic analytic silviculture techniques (Boyce 1977) to examine changes anticipated by natural forces unaffected by man (fig. *4)*. The dominant old trees are assumed to die, break, or blow down at about 290 to 310 years of age. Relatively small openings of less than 0.6 of an acre are formed. The seedling habitat (S) declines for about 30 years. Then, as the proportion of old growth (O) increases, mortality of the old trees increases the proportion of seedling habitats to less than 2 percent of the forest. Old-growth habitat increases to about 63 percent of the forest. After 170 years, each of the other habitats, other than old growth, occupies less than 10 percent of the forest.

Now we change the mode of management. The result is to increase the proportion of seedling habitats, reduce the proportion of old growth, and reduce the constraints on the distribution of habitats (fig. 5). With this mode of management, 30 percent of the area is permitted to rotate through a 200-year period and 70 percent of the area is permitted to rotate through a LOO-year period. Sizes of the openings are 10 ± 2.4 acres and are interspersed so that, in time, all of the kinds of habitats are intermingled. After 170 years, the sapling habitat covers the largest area, about 26 percent of the forest. All other habitats represent 4 percent for seedlings to 18 percent for pole-10 habitats.

Opening size is as important as the rate of harvest For anticipating the diversity of habitats. The size of openings formed by harvest determines, over time, the area of each kind of habitat, old growth as well as seedling. The amount of transition area, ecotone, between habitats is determined by the combinations of rate of harvest and opening size. For a given rate of harvest, the amount of ecotone increases as opening size decreases and deviates in shape from a perfect circle. Since harvest openings are almost never circular because of streams, roads, rocks, and other variables, opening shapes are typically variable

The interspersion of habitats is related to size of opening. If the annual rate of harvest is equal to the opening size, then only one opening is formed per year per forest type. As opening size declines from the annual rate of harvest, the number of openings per year increases and dispersion of habitats increases. If opening size becomes relatively small, less than about 3 acres, the Forest manager may choose to cluster the openings to reduce both the cost of road construction and the movement of sediment (Boyce 1977, page 16). The clustering of small openings reduces the dispersion of habitats in the forest. Small openings constrain the Livelihood for some plants and animals, and clustering of these openings increases the constraint.

One can anticipate the diversity of communities for an infinite number of other modes of management by changing the rates of harvest and the sizes of openings. More detail is given by Boyce (1577, 1578).

5. HOW TO RELATE DIVERSITY TO MULTIPLE BENEFITS

5.1 The Integration of Diversity and Benefits

In this section we describe how the relationships of diversity and benefits may be integrated to simultaneously analyze, estimate, and specify the consequences of alternative plans for multiple benefits.

From the theory for multiple benefits (Boyce 1977, In press), the proportional distribution of habitats determines the kinds of multiple benefits available from any specified forest area. The relative amount of a benefit may be estimated by algorithms scaled from 0 to 1 (figs. 1, 2, and 3). The algorithms for benefits are independent of each other but are totally dependent on the spatial and temporal diversity of habitats.

The diversity of habitats can be used to integrate benefits and to simultaneously examine the consequences of management actions. For the example used in previous sections (secs. 2.5 and 4.2), one can consider how no harvest of timber changes the diversity of seedling, sapling, pole-6, pole-8, pole-10, mature timber, and old-growth stands (fig. 4). And, one can consider how these changes affect the relative amounts of timber harvested; the relative livelihood for squirrel, deer, and bluebirds; and the relative amounts of sediment moved (fig. 10). Since no timber is harvested, the potential eimber index (T) is zero. The livelihood for deer (D) declines as the proportion of seedling habitat declines during the first 30 years. With an increase in the mortality of old trees, deer browse increases and the livelihood for deer increases to about 0.12. As the proportion of hard mast-producing trees increases, the livelihood for squirrels (Q) increases to 1 by year 50 and remains at this level for about 32 years. After year 80, the livelihood for squirrels declines as the dominant trees exceed the ages for producing large amounts of mast (U.S. Dep. Agric., Forest Service 1971).

Without timber harvesting, a reduction in open areas for bluebirds (L) to feed and nest reduces their livelihood to zero. And, since no roads are being constructed, increased sediment movement (I) is also zero. (Some sediment movement occurs, of course, under natural conditions.) The index (I) is a relative measure of the increased movement of sediment in relation to road construction.

Now, we change the mode of management to bring about the distribution of habitats described in figure 5 and in section 4.2. The availability of benefits (fig. 11) is now different from that for no timber harvest (fig. 10). The potential timber index (T) increases to about 0.75 of the maximum; the livelihood for deer (D) increases to about 0.70 of the maximum; the livelihood for squirrel (Q) increases to and remains at about 0.75 of the maximum; and the livelihood for bluebirds (L) increases to about 0.65 of the maximum. Sediment movement (I) increases to about 0.75 of the acceptable limit.

In this way, the diversity of plant and animal communities can be related to the suitability of a specific land area to meet overall multiple-use objectives. The objective for multiple-use management is not to produce so much timber, beef, water, game, recreation, hunting, fishing, and wilderness experience. Rather, the objective becomes a single goal, one of the various possible states of forest organization. For an interval of time the goal is to bring about the state of forest organization which determines a certain diversity of habitats and, thus, provides a biologically possible and desirable combination of benefits. This goal is biologically possible, physically attainable, and economically feasible.

BENEFIT INDEX (DIMENSIONLESS)

YEARS

```
                   .25             .5             .75             1. TIWL
   0T - - - - - - - -Q - - - - - - - D - - - - - - - - - - - - - - - TIL
    T              .  Q    D                                      . TIL
    T              D.  Q                                          . TIL
    T          D    .  Q                                          . TIL
    T         D     .   Q                                         . TIL
    T       D       .    Q                                        . TIL
    T      D              Q                                       . TIL
    T    D                  Q                                     . TIL
    T   D                    Q                                    . TIL
    T   D                     Q    .                              . TIL
 10 T -D- - - - - - - - - - - -Q- - - - - - - - - - - - - - - - - - TIL
    T D                            .  Q                           . TIL
    T D                                       Q    .              . TIL
    T D                                         Q .               . TIL
    T D                                            Q              . TIL
    T D                                            .Q             . TIL
    T  D                                           .  Q           . TIL
    T  D                                                 Q        . TIL
    T   D                                                    Q    . TIL
    T   D                                                       Q . TIL
 50.T - -D- - - - - - - - - - - - - - - - - - - - - - - - - - - - Q TIL
    T     D                                                       Q TIL
    T      D                                                      Q TIL
    T      D                                                      Q TIL
    T      D                                                      Q TIL
    T       D                                                     Q TIL
    T       D                                                     Q TIL
    T        D                                                    Q TIL
    T        D                                                    Q TIL
    T        D                                                   Q. TIL
    T        D                                                 Q  . TIL
 90.T - - - -D- - - - - - - - - - - - - - - - - - - - - - - - Q - - - TIL
    T         D                                           Q       . TIL
    T         D                                    .    Q         . TIL
    T         D                                    .   Q          . TIL
    T          D                                   .Q             . TIL
    T          D    .                            Q .              . TIL
    T          D    .                          Q   .              . TIL
    T          D    .                        Q                    . TIL
    T          D    .                      Q                      . TIL
    T          D    .                   Q                         . TIL
130.T - - - -  D - - - - - - - - - -  Q - - - - - - - - - - - - - - TIL
    T          D    .              . Q                            . TIL
    T          D    .              .Q                             . TIL
    T          D    .              Q                              . TIL
    T          D    .              Q                              . TIL
    T          D    .              Q.                             . TIL
    T         D                    Q.                             . TIL
    T         D                  Q .                              . TIL
    T         D                  Q .                              . TIL
    T         D                  Q .                              . TIL
        - - -D- - - - - - - - - -Q - - - - - - - - - - - - - - - - TIL
```

Figure 10.--When no timber (T) is harvested, some benefits such as the livelihood for deer (D), bluebirds (L), and, in time, squirrel (Q), are constrained. The relative amount of constraint of the habitats from complete randomness is indicated by the rising constraint quanta (*) for habitats (fig. 4).

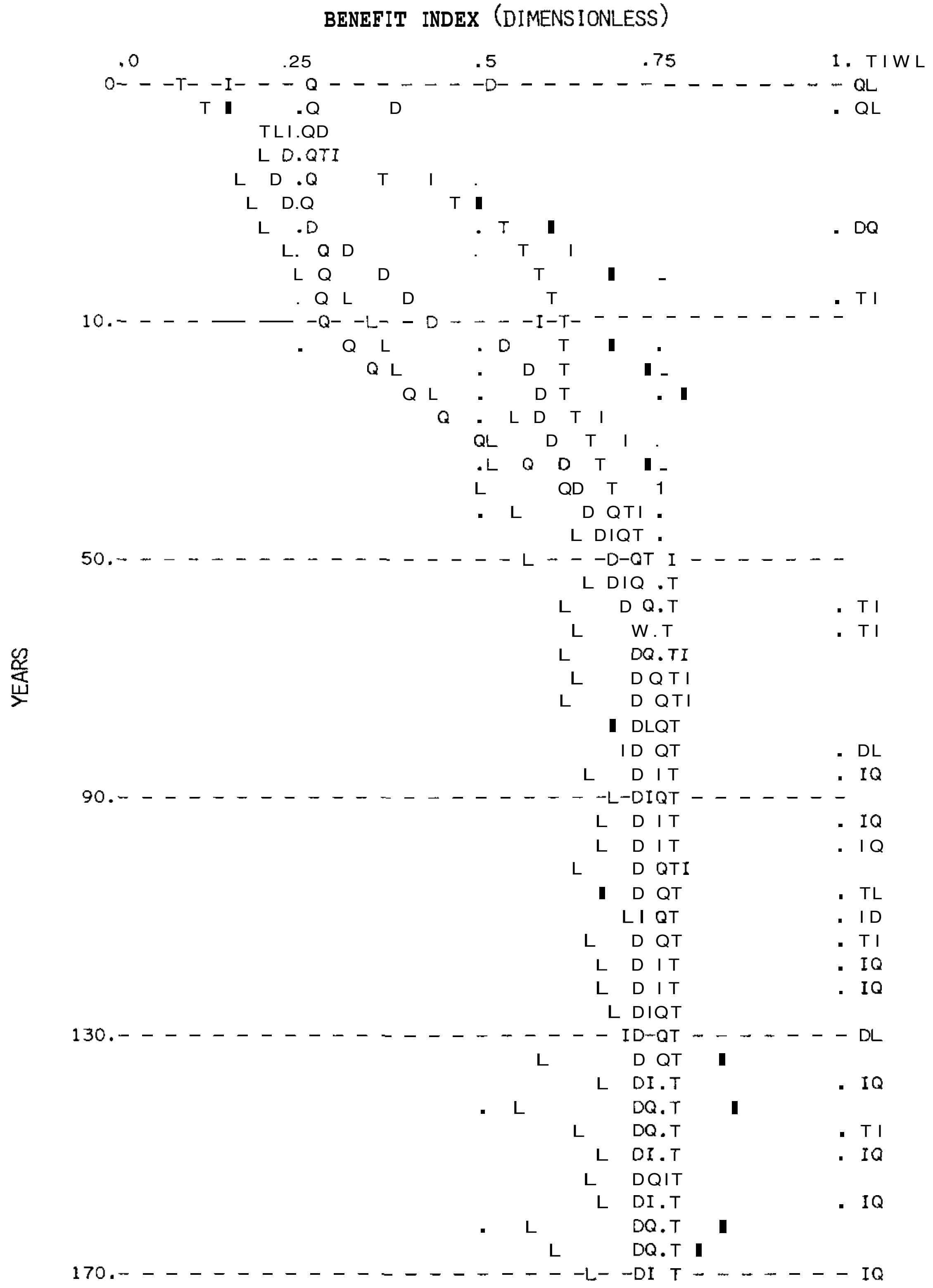

Figure 11.--Indices for eight benefits and one impact for a moderate mode of management. T = potential timber index; I = sediment; D = deer habitat; Q = squirrel habitat; L = bluebird habitat. This illustration is modified from figure 2 (Boyce 1977). Indices are plotten annually for the first 10 years, then at 4-year intervals. Letter groups at the top of the graph indicate coincident indices; the first letter of *each* group appears on the plot.

The organization of the forest (the distribution of habitats) is controlled by scheduling the rates of harvest and the size of openings formed by harvesting (Boyce 1977, 1978). Two or more rotation periods may be superimposed so that old growth and young stands are closely intermingled and, over time, interchangeable. Thus, age classes of stands are distributed in varying proportions from 1 year to some very old age such as 300 years. The distribution of habitats is brought to one of a large number of steady states. At any one of a number of steady states, a livelihood for most, **if** not all, endemic organisms is possible and certain combinations of benefits are available.

In this way, plans can include the results of integrated analyses and anticipated consequences of alternative modes of management.

5.2 Monitoring Diversity for Multiple-Use Objectives

The purpose for monitoring diversity is to acquire information that is useful for making decisions about the congruence of an implemented plan and the real forest. By congruent we mean that actions selected under the plan direct the biological systems to achieve the desired state of forest organization (Boyce, In press). An important way to monitor diversity is to use periodic inventories of the forest to compare the diversity of elements in the real forest with those anticipated by the plan.

The period for forest management is separated into management intervals, typically 10 years. At the beginning of each interval the forest is inventoried for those elements of diversity that indicate the state of organization. The plan anticipates a future state of forest organization; for example, the diversity of habitats (fig. 5). Data from these inventories are used first to examine the congruence of the plan and the habitats. For example, one may use a chart (fig. 6) to compare the proportional distributions of seedling, sapling, and other habitats at time 10 years in the plan (fig. 5) with data from the inventory. Reasons for differences are determined and, if necessary, adjustments are made in the plan (Boyce 1977, page 19).

During the 10-year management intervals, information from research, observations, and experience are used to adjust the algorithms for benefits to fit the specific forest that is under management. For example, the shape of the curves in figures 1, 2, and 3 may be changed to agree with new findings. An additional algorithm may be added for the computation of a combined index (sec. 2.2). New yield tables may be developed for timber. Algorithms may be developed for additional benefits, including streamflow, social values, and economic cost and returns. The new inventory and the revised algorithms are inserted into the plan; for example, one of the DYNAST modes of management (Boyce 1977, 1978). The anticipated combinations of benefits for the next 10 to 100 years is examined. The benefits are then evaluated in terms of consumer attitudes.

New attitudes and desires for social and economic benefits may require a change in the mode of management. These changes are made by adjusting the rates of timber harvest and the sizes of openings for each forest type to bring about the desired combination of benefits (Boycr 1977). For the next 10 years, the management goal is to change the present state of forest organization toward that anticipated by the revised plan.

Near the end of each management interval, the processes of inventory, algorithm adjustment, and change in management mode are repeated. In this way, monitoring provides information that is useful for making management decisions about the congruence of the plan and the real forest. The multiple-use objectives are kept congruent with consumer attitudes for social and economic benefits.

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The National Forest Management Act of 1976 (90 Stat. 2949; 16USC1600) chartered a new direction for the Forest Service. Previously, no regulations existed that provided for a diversity of forest plant and animal communities and the preservation of indigenous tree species, nor were consumer attitudes regarding social and economic benefits and multiple-use of forests so clearly delineated. The Act necessitated, first of all, the development of an operational definition of "diversity" that would have a common meaning to foresters and forest managers. This Paper provides such a definition and sets forth new concepts and applications of forest management designed to bring about the improvements desired.

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The Forest Service. U.S. Department of Agriculture,is dedicated to the principle of multiple management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forest and Grasslands, it strives - as directed by Congress - to provide increasingly greater service to a growing Nation.