Chapter 28.

Monitoring Tree Species Diversity

over Large Spatial and Temporal Scales

James F. Rosson, Jr. and
Clifford C. Amundsen[1]

Abstract—*The prospect of decline in biological diversity has become a central concern in the life sciences, both around the world and across the United States. Anthropogenic disturbance has been identified as a major factor affecting species diversity trends. An increase in the harvesting of naturally diverse timber stands in the South has become an important issue. The ultimate impact of this high, and increasing, level of disturbance on tree species diversity in forests of the Southern United States is uncertain. We offer a brief review of literature related to major points in the development of species diversity concepts over the last 100 years. This is followed by a case study that makes use of periodic U.S. Department of Agriculture Forest Service, Forest Inventory and Analysis (FIA) data from Mississippi. Our interest, for southern forests, is whether tree species richness has declined, increased, or remained essentially stable over the last 35 years. We find that tree species richness has declined by 11 percent across Mississippi since 1977. However, in FIA plots that had no evidence of harvesting, tree species richness increased by 44 percent since 1967. It is difficult to determine what constitutes a healthy level of tree species richness for particular sample designs and large-scale State surveys. Additional analytical complexity comes from the lack of documentation and knowledge concerning various levels of richness dynamics for large spatial and temporal scale studies.*

INTRODUCTION

Questions about, concerns about, and interests in biological diversity have reached high levels of priority with academics, research scientists, resource conservationists, political decisionmakers, civic leaders, and interested members of the general public (particularly those in the environmental community). Though biological diversity has been of interest to ecologists for many decades, broader popular interest in the subject developed in the 1980s in response to the highly publicized exploitation and deforestation of tropical rain forests (Wilson and Peter 1988). This disturbance takes the form of intensive and extensive timber harvesting and land clearing. Heightened public interest in biological diversity and the decline of tropical forests was reflected in the 1986 National Forum on Biodiversity (Wilson and Peter 1988).

Anthropogenic disturbance on forest land in the United States, and its long-term effects on forest biology, has also received considerable attention (Hunter 1999, Kimmins 1997, Kohm and Franklin 1997, Maser 1994, Noss and Cooperrider 1994, Perry 1994, Szaro and Johnston 1996). The types of disturbance range from permanent clearing, as in the conversion of forest land to urban or agricultural use (in this context permanent may mean only a few years to many decades), to intense and repeated harvesting activity. Increases in timber harvesting in the Southern United States has raised concerns about the long-term sustainable (both productive and ecologically sound) use of the forest resource. The concept of sustainable use is different from its predecessor, sustainable yield, in that equal weight is given to biological, social, economic, and political components, whereas sustainable yield matches levels and rates of harvesting with maximum rates of species production. See Campbell (2002) for more background on sustainability.

[1] Research Forester, U.S. Department of Agriculture Forest Service, Southern Research Station, Knoxville, TN 37919; and Professor, University of Tennessee, Ecology and Evolutionary Biology, Knoxville, TN 37996, respectively.

Increases in timber harvesting on private land in the Southern United States have resulted primarily from a combination of consumer demands and reductions in the amount of public-lands timber being offered for contract sales. The latter follows from reductions in the allowable sale quantity [the amount of timber offered for sale on national forests by the USDA Forest Service (Forest Service)]. These reductions in timber being offered for sale can be attributed to issues related to habitat protection (as for the spotted owl in the Northwestern United States), reductions in budget and staff, and increases in the amount of time and money expended in litigation (Kohm and Franklin 1997). The result is that less timber is being removed from national forest lands, particularly in the West. The Southern United States is making up much of the shortfall in western timber production by increasing harvests on forest industry and nonindustrial private forest lands. Currently, the Southern United States accounts for 65 percent of all tree volume harvested in the United States (Smith and others 2001). This is a substantial increase since 1992, when the South contributed 55 percent of all harvested volume (Powell and others 1993).

The issues of sustainable forests and sustainable forestry involve both short- and long-term impacts. An example of short-term impacts would be timber supply shortages while long-term impacts reflect the integrity of forest biology. The latter include, but are not limited to, soil deterioration, habitat destruction and alteration, changes in stand structure, successional interruptions, stand fragmentation, declines in old-growth area, age-class imbalance, changes in species composition, and impacts on overall biological diversity. Noss (1996) has identified seven types of biotic impoverishment in forests. These can be thought of as trajectories of change as the dynamics of natural forest processes are shifted by more intense management. The changes are: older stands to younger stands, structurally and compositionally complex stands to simple stands, large continuous forests to smaller fragmented patches, forest stands that are in close proximity to each other (or are continuous with) to increasingly isolated patches, frequent cool fires to fewer hot fires, few roads to many roads, and stable species populations to more endangered species. Any of these factors may occur independently or in combination.

As forest harvesting activity in the Southern United States continues to increase, decisionmakers will need reliable information that tracks the impact of harvesting on forest resource integrity. In order to evaluate the long-term impact of intense timber harvesting, decisionmakers need to know how tree species diversity and overall forest composition may be affected. The effect an increasing area of artificially regenerated forest stands will have on species diversity over a large area, such as a State, is a related concern. For conservation strategies to be effective, reliable information about species diversity trends must be available. Traditional ecological studies have in most cases dealt with smaller areas. However, extrapolations from small-scale, independent, and scattered studies do not provide adequate and reliable information about conditions and processes over large spatial scales.

The study of biological diversity is not new. This chapter presents a brief chronological review of the diversity concept as it has developed in the United States over the last century. We then discuss preliminary findings of a large-scale diversity assessment for an extensive forest area in the Southern United States, along with considerations that are important when applying such assessments over large geographic regions. A case study based on data from recent forest surveys of Mississippi is used to illustrate a method of tracking tree species richness over time.

HISTORICAL OVERVIEW OF THE DIVERSITY CONCEPT IN THE UNITED STATES

Much of the species diversity work after the 1950s was aimed at devising new mathematical methods for quantifying diversity assessments. This review does not cover the broad range of studies devoted exclusively to that subject. Additionally, a general lack of standardization in the terminology may cause some confusion. In this chapter, we use the terms richness and species diversity interchangeably, but we recognize that richness is one type of measurement attribute describing species diversity (Magurran 1988, Pielou 1974). Richness has traditionally been defined as the number of species occurring in a specific area. This area may be small or large. It is important to understand how the richness measure (or any other species diversity measure) is obtained because results obtained from applying different sample designs to the same sample population have differed considerably (Diserud and Aagaard 2002).

Earlier, the concept of species diversity was regarded as a historical phenomenon related to the accumulation of species over time (Fischer

1960, Wallace 1876, Willis 1922). What is now called the study of species diversity was considered as part of the study of species abundance and species populations. Much of the interest and early work in species abundance was by animal ecologists (Kingsland 1985). The early part of the 20th century also saw the beginning of development of techniques for describing plant communities in quantitative terms. Examples include the works of Clements (1905), Gleason (1920), Cain (1932), and Braun (1935). Oosting (1956) described the difference between two approaches to analysis—descriptive (analytical) statistics and qualitative (synthetic) statistics. Descriptive statistics involved measures of individual stands (the actual concrete community that could be visualized on the ground); qualitative statistics were estimates of measures of several stands in aggregate (the abstract community type composed of disjunct stands).

Jaccard (1912) was the first to demonstrate that there was an increase in the number of species with an increase in area (Goodall 1952). This was later expressed mathematically by Arrhenius (1921). Application of the terms "rich" and "poor" is usually credited to Baker (1918), who recorded the number of species on lake bottoms. Thienemann, a limnologist in Europe, identified three important species-abundant principles: (1) the greater the variety of habitats, the larger the number of species; (2) the more that conditions deviate from the normal optima for most species, the smaller is the number of species that occur and the greater the number of individuals that do occur; and (3) the longer a habitat has been in the same condition, the richer and more stable is the community (Goodman 1975, Hynes 1972). The third of these principles is now known as the stability-diversity hypothesis, and is still studied and strongly debated today.

Elton (1927) and others realized that species numbers and diversity were most likely a part of important principles in plant and animal ecology, but Elton observed that it was not clear what these important principles entailed (McIntosh 1985). Publication of Thienemann's first two principles led other workers to conduct a long series of studies involving species-area relations. Cain (1938) and Preston (1948) were early investigators of species-area curves. The early work dealing with mathematical properties of species-area relations has been reviewed by Connor and McCoy (1979). By carefully counting species, several investigators were able to demonstrate that species were organized into predictable compositions (at least at the guild level) and structures (Gleason 1922; Preston 1948; Williams 1944, 1953). Many early works showed that a majority of species were rare and less abundant, and that only a few species were dominant or very abundant. Ecologists soon found it was not possible to conduct a census of an entire biotic community and that patterns of dominance and species abundance would have to be detected by sampling (Golley 1993). Graphing the number of species observed against the number of individuals on a logarithmic scale often produced a straight line. Supposedly, the slope of this line was a measure of the species diversity of the community (Fisher and others 1943). Pielou (1977) states that this approach to species diversity analysis was first introduced by Fisher in 1943. Margalef's later work (1958) was instrumental in the popularization of the phrase "species diversity" among ecologists (Green 1979). Although much work had been done on species diversity up through the 1950s, no ecology textbooks of the 1940s and 1950s, with the exception of Odum's textbook (1959), even mentioned the term "diversity" (Schluter and Ricklefs 1993).

In 1969, the famous Brookhaven Symposia in Biology maintained that the continuity and sustainability of life systems appeared to be associated with the number of species per unit of area (Wolda and others 1969). This meeting also ensured the popularization of the term "diversity." By the late 1960s the study of diversity was expanding, involving not only the number of species but also the proportionate distribution of individuals (evenness) and the consequent development of a myriad of diversity indices. This period also marks the beginning of a significant number of diversity study contributions to the literature. Lloyd and Ghelardi (1964) are credited with introducing use of the term "evenness" in the context of diversity (Krebs 1989).

The beginning of the modern era of quantitative ecology has been attributed to MacArthur (McIntosh 1985). Building on Preston's work (Preston 1948) concerning the canonical distribution of species, MacArthur and Wilson expanded upon Preston's idea as the basis for their seminal book "Theory of Island Biogeography" (1967). Ideas developed in this book essentially set the stage for much of the ecological work over the next two to three decades. Many workers in either plant or animal ecology borrowed and built upon MacArthur's ideas and work related to species-area and species-distribution phenomena.

The literature related to species diversity studies and technique development over the last several decades is voluminous. Many papers in the literature have dealt with the development of new and improved measures of diversity. Several papers and books are considered seminal and helped clarify and resolve certain issues pertaining to the problems of measuring and analyzing species diversity data. Examples are Pielou (1969, 1975), Peet (1974, 1975), and Hurlbert (1961). A comprehensive summary of the diversity literature, prior to 1979, has been prepared by Dennis and others (1979).

Diversity analysis was incorporated into many ecological studies after the 1960s, and increases in tropical forest land clearing and growth of the environmental movement stimulated interest in species diversity along with genetic diversity, habitat diversity, landscape diversity, and ecosystem diversity. In the United States, questions were raised about the management of national forests. One particular concern was the conversion of hardwood stands to pine stands. To address this concern, language identifying the need to preserve natural diversity was written into the National Forest Management Act of 1976. An important workshop addressing this issue was held in 1982 (Cooley and Cooley 1984).

Prominent biologists were quick to address global threats to diversity. This resulted in the National Forum on Biodiversity, which took place in Washington, DC, in September 1986 (Wilson and Peter 1988). The published proceedings of this meeting were distributed widely and quickly brought national and international attention to the potential problem of declining species diversity and the ultimate loss of species through extinction. Since then a followup volume "Biodiversity II" has been published, covering such topics as how scientists study diversity, the status of existing knowledge about life on Earth, and a series of key questions that remain unanswered (Reaka-Kudla and others 1997).

Since the National Forum on Biodiversity, other important conferences have been held. These include the International Symposium of Ecological Perspective of Biodiversity which took place in Kyoto, Japan, in December 1993 (Abe and others 1997); the Symposium on Biodiversity in Managed Landscapes: Theory and Practice, held in Sacramento, CA, in July 1992 (Szaro and Johnston 1996); the Sixth Cary Conference, held in May 1995 at the Institute of Ecosystem Studies, Millbrook, NY (Pickett and other 1997); and the plenary sessions of the 45th annual meeting of the American Institute of Biological Sciences at Knoxville, TN, in August 1994. The last resulted in the publication of a supplementary issue of the journal "Bioscience" (Bioscience 1995). These meetings and published proceedings focused on educating the public about the importance of biodiversity, described the current state of knowledge in particular disciplines, and provided examples of failures and successes in managing ecosystems to preserve biological diversity while maintaining economic viability (Powledge 1998).

Several books about diversity have been published over the last few years. Examples include "Species Diversity in Space and Time" (Rosenzweig 1995), "Species Diversity in Ecological Communities" (Ricklefs and Schluter 1993), "Biological Diversity" (Huston 1994), "Precious Heritage: The Status of Biodiversity in the United States" (Stein and others 2000), "Saving Nature's Legacy: Protecting and Restoring Biodiversity" (Noss and Cooperrider 1994), "Maintaining Biodiversity in Forest Ecosystems" (Hunter 1999), "Ecological Diversity and its Measurement" (Magurran 1988), "The Unified Theory of Biodiversity and Biogeography" (Hubbell 2001), "Global Biodiversity Assessment" (Heywood 1995), "Global Biodiversity: Status of the Earth's Living Resources" (Groombridge 1992), and "Biodiversity: A Biology of Numbers and Difference" (Gaston 1996). All are comprehensive in scope and include sizeable reference sections. Huston's reference section covers 98 pages. The list above is not complete but provides an entrance into the literature.

Although much work has been completed on the theory and concepts of biological diversity, little has been done on the application of this theory to real world problems. The literature is based largely on incidental observations or reports rather than detailed systematic and analytical evaluations. Studies dealing with comparative analysis are valuable and rare (Machlis and Forester 1996).

Most of the studies that have been undertaken were done in small areas that had attracted investigators' attention, mostly because these sites had unusual biotic or abiotic characteristics. The cost in time and money of sampling across areas larger than a few hundred hectares is often prohibitive. Examples of plant patterns and responses to anthropogenic disturbance in forests at a small scale can be found in Grime

(1979), Oliver (1981), and Hunter (1990). Certain workers, such as Sites and Crandall (1997) and Skov (1997), have implemented novel approaches to biodiversity studies. Quantitative studies using systematic and analytical techniques on a large regional scale (an area the size of a State or larger) are lacking (Langer and Flather 1994, LaRoe and others 1995). There have also been requests for the establishment and application of rigorous standardized sampling and analytical techniques for biodiversity assessments (Debinski and Humphrey 1997, Solomon 1979).

Because of the cost and complexity of sampling large continuous geographic areas, very little, and very limited, data (usually addressing only specific resource and conservation issues) are available for large regional studies. Some investigators have taken several local studies and extrapolated the results to a larger area or continental region. One example is a study by Glenn-Lewin (1977) in which richness information data from six temperate forest communities across North America were analyzed for correlations across large spatial scales in species diversity within ecosystem and community structure. Other studies have also followed a similar approach, either by aggregating several local studies scattered across a region or by using abstract information from flora listings by county (Currie 1991, Currie and Paquin 1987, Monk 1967). Although such efforts provide much-needed information, these studies lack rigor because they are based on nonprobability samples and because they have too few plots (from a regional perspective). Additionally, the data come from studies that poorly represent the whole of vegetation conditions and complexes across large areas.

There have been few definitive descriptions of diversity of temperate tree species in relation to disturbance over areas as large as a State. Only one study has attempted to evaluate these relationships over large geographic areas; Stapanian and others (1997) used data from Forest Service Forest Health Monitoring plots, but these data were incomplete because only 14 States were included in the program at the time of the study and because there were fewer than 150 forested plots (on average) for each State. It is questionable whether this small number of initial sample plots is sufficient to represent an area as large and diverse as a State. Additionally, such a small number of plots severely limits any attempt to poststratify the data. Since implementation of the Forest Health Monitoring Program has only recently begun, no adequate historical data are available. Therefore, trend analysis of species diversity is very limited at this time with these datasets.

Beyond the timber supply issue, concerns have been raised about the sustainability of the entire biotic and abiotic forest base. Several recent books have documented the urgent need to alter forest management practices to achieve certain conservation goals (Hunter 1980, Huston 1994, Kohm and Franklin 1997, Noss and Cooperrider 1994, Szaro and Johnson 1996). The Forest Service has adopted and implemented the concept of ecosystem management in order to protect and provide sustainability for all attributes of forests. Foremost in these new approaches to forest management is the concept of managing forests in a way that protects and fosters the establishment of natural biodiversity. With the establishment of the biosphere initiative, the Ecological Society of America has brought the biodiversity problem to the public forum and to the attention of policymakers (Lubchenco and others 1991). Additionally, the dialog has gone beyond the biological aspect of the diversity issue to include and quantify the economic benefits of a diverse natural world (Freeman 1998).

There has been much speculation about the impact of timber harvesting on forest biology, most of it based on studies of small stands. Application of a probability-based sample would provide meaningful insight into the status of any State's forests. Some investigators have concluded that the status of species diversity in U.S. forests has improved dramatically during the last century (Salwasser and others 1992). Others are convinced that the degradation of entire ecosystems is continuing (Noss and others 1994). No studies or rigorous statistics that accurately document the status of biodiversity over large areas in the United States are available (LaRoe and others 1995, Noss and Cooperrider 1994, U.S. Environmental Protection Agency 1990). Therefore, neither claim can be supported rigorously.

Resources for tightly focused large-scale research efforts to evaluate trends in diversity are lacking. Therefore, it seems appropriate to adapt and employ existing large-scale data, particularly if it is rigorously assembled, for the analysis of diversity dynamics. Such data, although originally assembled for use in timber inventory studies and quantitative interpretation, exist in the continuous forest inventory records of the Forest Service, Forest Inventory and Analysis (FIA). These data, which have been collected under conditions that allow their validity to be tested, can be used to demonstrate diversity trends and dynamics over a large spatial scale over a considerable period of time. Below, we analyze such data for the State of Mississippi.

A CASE STUDY OF DIVERSITY TRENDS IN A SOUTHERN FOREST

Data for Mississippi were used as a source of information about changes in tree species diversity over time. The data were from the FIA Program and consisted of field plot data collected over the last 35 years during four survey measurements (1967, 1977, 1987, and 1994). Field plots in which tree harvesting occurred were considered as having undergone experimental manipulation; plots in which there was no harvesting during the four survey measurements were considered the control. This methodology—that of treating natural or anthropogenic disturbance as the manipulation stage of an experiment—is useful in situations in which it is impractical to conduct a true experiment (Hairston 1989, Scheiner 1993).

The study consisted of two phases. In the first phase, all of the plots in the statewide sample were considered without any regard to poststratification criteria. Levels of tree species diversity for the four survey measurements were compared. In the second phase, only sample plots that had not been harvested during the period covered by the four survey measurements were considered. The null hypothesis, that there was no difference in tree species diversity over the four survey measurements made in 1967, 1977, 1987, and 1994, was tested for both the total plot dataset and the undisturbed plot dataset with parametric statistics. The repeated measures analysis-of-variance procedure was used for the tests, with significance established at the 0.05-percent level.

Only trees larger than or equal to 12.7 cm in diameter at breast height were included in the analysis. An overview of the forest survey sample design used in Mississippi has been described by Rosson (2001). The diversity measure used was species richness, defined as the total number of different species occurring on each survey sample unit (field plot). This was a departure from traditional practice, in which the species richness count is typically the sum of different species occurring on all of the sample units. An advantage of analyzing the richness count by sample unit was that this procedure made it possible to utilize parametric statistical tests. Additionally, this methodology reduced the effect of overweighting the loss of one or two species. This was especially important in this study because the low sampling intensity over a large scale means that the forest survey sample design does not adequately sample rare or infrequently occurring species. Preston (1948) has shown how sampling fails to capture the entire spectrum of species. There will always be a percentage of species that occur so infrequently that they will not be detected by sampling. In large-scale assessments it is important that richness measures reflect overall shifts across a State. The occurrence or nonoccurrence of one species on only one sample plot may reflect only a uniqueness of the sample design, and not a biological event.

RESULTS AND DISCUSSION

Disturbance Background

Between 1977 and 1994, 4.1 million ha of Mississippi timberland underwent some form of harvesting.[2] A harvest was defined as any harvesting activity in which all, or a high proportion, of the manageable stand was removed, thereby marking the beginning of a new stand rotation. Examples of types of harvests are partial harvests (which would include various selection methods), seed tree, shelterwood, high-grade, and clearcut harvests, as defined by Smith (1962). In addition to these harvested areas, another 0.9 million ha of timberland underwent cutting in an intermediate stand treatment such as thinning or stand improvement.

Of the 4.1 million ha harvested in Mississippi, 1.6 million ha were clearcut (see footnote 2). Clearcutting often has the greatest potential effect on altering tree species diversity. This is because natural stands that are harvested are frequently replaced with monospecific softwood plantations. Management programs typically favor only one species in plantations. In addition, harvest cycles may become shorter and shorter.

The clearcut acreage was spread fairly evenly across Mississippi, with the exception that clearcut acreage was lower in the northwest portion of the State (fig. 28.1) (see footnote 2). Between 1977 and

[2] Rosson, James F., Jr. Current stand characteristics of Mississippi timberland harvested between 1977 and 1994. 21 p. Manuscript in preparation. On file with: Southern Research Station, Forest Inventory and Analysis, 4700 Old Kingston Pike, Knoxville, TN 37919.

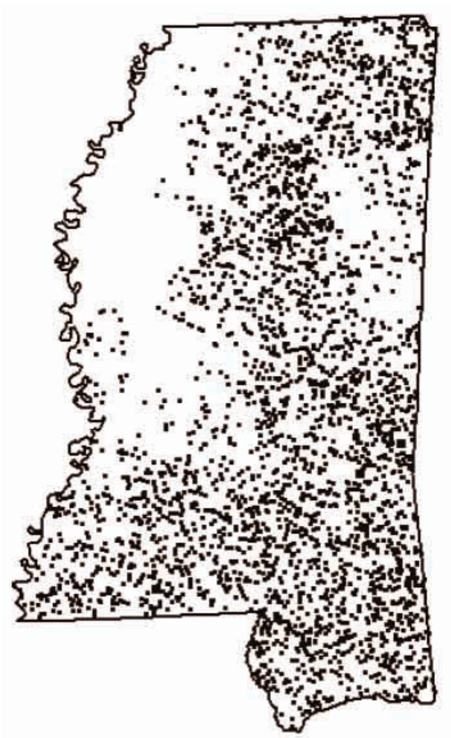

Figure 28.1—Spatial distribution of clearcut timberland in Mississippi. Each dot represents 500 ha of clearcut timberland, harvested between 1977 and 1994. During this period, 1.6 million ha were clearcut.

1987, 0.6 million ha of new softwood plantations were established; another 0.4 million ha were established between 1987 and 1994. Currently, there is a total of 1.7 million ha in softwood plantations throughout Mississippi.[3] The direct effect of these monocultural plantations was to reduce average tree species diversity in the State.

Tree Species Diversity Dynamics

Mean tree species richness estimates, across Mississippi, for all sample units combined were 4.53, 5.02, 4.82, and 4.49 species per sample unit for survey years 1967, 1977, 1987, and 1994, respectively (fig. 28.2). There was not a significant difference between richness in 1967 and richness in 1994 (df = 2,805, $p < 0.0617$). The change in richness from 1977 to 1994 was highly significant (df = 2,805, $p < 0.0001$); note that significant is ($0.05 \geq p > 0.01$); very significant is ($0.01 \geq p > 0.001$), and highly significant is ($p \leq 0.001$) (Sokal and Rohlf 1995).

In contrast, tree species richness means for sample units without any harvesting disturbance were 4.73, 5.86, 6.49, and 6.80 species per sample unit for 1967, 1977, 1987, and 1994, respectively (fig. 28.3). The increase in richness between 1967 and 1994 was highly significant (df = 552, $p < 0.0001$).

Tree species richness for all sample units combined increased between 1967 and 1977. Thereafter, richness declined in every survey

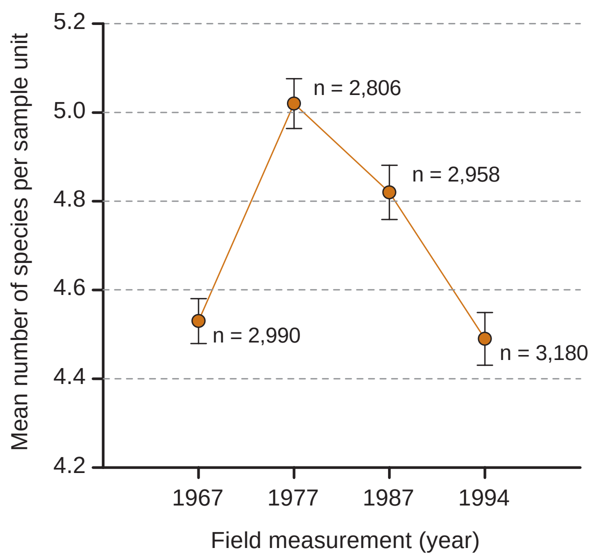

Figure 28.2—Mean species richness per sample unit for Mississippi, by survey year, for all sample units. The error bars represent 2 standard errors of the mean.

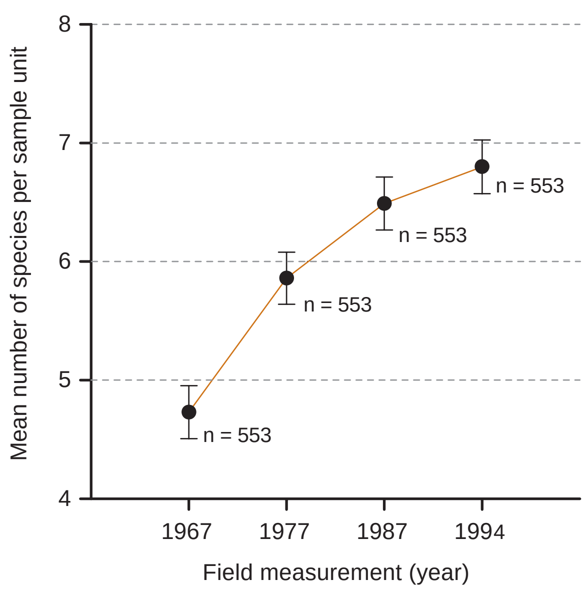

Figure 28.3—Mean species richness per sample unit for Mississippi, by survey year, for sample units that had no evidence of harvesting disturbance during the four survey measurements. The error bars represent 2 standard errors of the mean.

[3] Rosson, James F., Jr. The status of forest plantations in Mississippi, 1994. 30 p. Manuscript in preparation. On file with: Southern Research Station, Forest Inventory and Analysis, 4700 Old Kingston Pike, Knoxville, TN 37919.

measurement. One possible explanation for this was that the forests of Mississippi, within that period, were recovering from the heavy cutting that ended in the 1930s. Species richness had, most likely, been increasing through the decades that followed that cutting. It was during the late 1960s and 1970s that a new wave of timber harvesting began. The peak of more than five species per plot in 1977 (fig. 28.2) may indicate the end of the recovery period and the beginning of a new period of decline in species richness. The analysis is complex because there is no adequate source of baseline data with which to compare results. We do not know what constitutes a normal, healthy level of tree species richness for this particular sample design. The undisturbed sample units were the only applicable benchmark for potential tree species richness in Mississippi, and one should recognize that factors other than harvesting could have affected richness. Examples of such factors might include ownership (and owner objectives), site, and stand history. Moreover, the stage of succession will also affect the number of species per plot. Some forest stands that are in midsuccessional stages may have the highest richness because they contain early, mid, and late-successional species.

Demonstrating a significant difference between means without considering the ecological relevance of the difference may be trivial. Recent literature has emphasized the importance of the distinction between biological and statistical significance (Hilborn and Mangel 1996, Krebs 1989, Scheiner 1993). In our study, we consider the change in tree species richness to be both biologically and statistically significant, based on the following. First, the same sample units were remeasured during each survey year. Second, and most importantly, the sample design remained the same throughout all four measurements. The same sample unit points were remeasured and the same basal-area prism factor was used throughout. It is also very important that the species lists for all the survey periods were the same. This meant grouping some species from the recent, more detailed, surveys to match those of older surveys (when there was less emphasis on tallying species of lesser economic importance). See Rosson (1999) for further details.

Use of remeasured plots helps eliminate much of the variation that is inherent in natural populations. High levels of variation can mask some true biological differences, so reducing this variation as much as possible improves the rigor of the study (Hayek and Buzas 1997, Husch and others 1982). In monitoring studies, the best estimates of variables used to detect change, such as density and basal area, are provided by the use of permanent, remeasured sample units (Bonham 1989). Second, the magnitudes of richness change (usually more than 3 percent), together with the size of the sample and a very low standard error, further support the evidence of real biological shifts in trees species richness. Finally, the comparison of the undisturbed sample units with all the sample units combined empirically supports the overall decline in tree species richness since the 1977 survey measurement.

The fact that tree species richness has increased significantly on sample units without harvesting supports the premise that harvesting disturbance is the major contributing factor in the decline of tree species richness. However, it is important to note that the study did not, nor was it designed to, find a causal agent of decline in richness. The study only points out that tree species richness has declined significantly over time and that concurrent harvesting disturbance is probably a major contributing factor.

There are no established criteria or guidelines for determining what level of tree species richness is too low for an area as large as a State. Also, we do not know the degree to which tree species richness varies naturally. Finally, little is known about the resiliency of mixed forest stands to the disturbances to which they are being exposed. Further work needs to be done in these areas before the results of tree species richness monitoring can be utilized in a rigorous and meaningful manner.

LITERATURE CITED

Abe, T.; Levin, S.A.; Higashi, M., eds. 1997. Biodiversity: an ecological perspective. New York: Springer-Verlag. 294 p.

Arrhenius, O. 1921. Species and area. Journal of Ecology. 9: 95–99.

Baker, F.C. 1918. The productivity of invertebrate fish food on the bottom of Oneida Lake with special reference to mollusks. Tech. Publ. 9. Syracuse, NY: Syracuse University, New York State College of Forestry. [Number of pages unknown].

BioScience. 1995. Science and biodiversity policy. [Place of publication unknown]: [Publisher unknown]. [Number of pages unknown]. Suppl. to Bioscience, American Institute of Biological Sciences.

Bonham, C.D. 1989. Measurements for terrestrial vegetation. New York: John Wiley. 338 p.

Braun, E.L. 1935. The vegetation of Pine Mountain, Kentucky. American Midland Naturalist. 16: 517–565.

Cain, S.A. 1932. Studies on virgin hardwood forest. I. Density and frequency of the woody plants of Donaldson's Woods, Lawrence County, Indiana. Proceedings of the Indian Academy of Sciences. 41: 105–122.

Cain, S.A. 1938. The species-area curve. American Midland Naturalist. 19: 573–581.

Campbell, L.M. 2002. Science and sustainable use: views of marine turtle conservation experts. Ecological Applications. 12(4): 1229–1246.

Clements, F.E. 1905. Research methods in ecology. Lincoln, NE: University Publishing Co. 334 p.

Connor, E.F.; McCoy, E.D. 1979. The statistics and biology of the species-area relationship. American Naturalist. 113: 791–833.

Cooley, J.L.; Cooley, J.H., eds. 1984. Natural diversity in forest ecosystems. Proceedings of the workshop. Athens, GA: University of Georgia, Institute of Ecology. 290 p.

Currie, D.J. 1991. Energy and large-scale patterns of animal-species and plant-species richness. American Naturalist. 113: 791–833.

Currie, D.J.; Paquin, V. 1987. Large-scale biogeographical patterns of species richness in trees. Nature. 329(24): 326–327.

Debinski, D.M.; Humphrey, P.S. 1997. An integrated approach to biological diversity assessment. Natural Areas Journal. 17(4): 355–365.

Dennis, B.; Patil, G.P.; Rossi, O. [and others]. 1979. A bibliography of literature on ecological diversity and related methodology. In: Grassle, J.F.; Patil, G.P.; Smith, W.K.; Taillie, C., eds. Ecological diversity in theory and practice. Fairfield, MD: International Co-Operative Publishing House: 319–353.

Diserud, O.H.; AaGaard, K. 2002. Testing for changes in community structure based on repeated sampling. Ecology. 83(8): 2271–2277.

Elton, C.S. 1927. Animal ecology. London: Sidgwick and Jackson. 207 p.

Fischer, A.G. 1960. Latitudinal variations in organic diversity. Evolution. 14: 64–81.

Fisher, R.A.; Corbet, A.S.; Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology. 12: 42–58.

Freeman, A.M., III. 1998. The economic value of biodiversity (letters). Bioscience. 48(5): 339.

Gaston, K.J., ed. 1996. Biodiversity: a biology of numbers and difference. Oxford: Blackwell Science. 396 p.

Gleason, H.A. 1920. Some application of the quadrat method. Bulletin of the Torrey Botanical Club. 47: 21–33.

Gleason, H.A. 1922. On the relation between species and area. Ecology. 3(2): 158–162.

Glenn-Lewin, D.C. 1977. Species diversity in North American temperate forests. Vegetatio. 33(2/3): 153–162.

Golley, F.B. 1993. A history of the ecosystem concept in ecology. New Haven, CT: Yale University Press. 254 p.

Goodall, D.W. 1952. Quantitative aspects of plant distribution. Biological Review. 27: 194–245.

Goodman, Daniel. 1975. The theory of diversity–stability relationships in ecology. Quarterly Review of Biology. 50(3): 237–266.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. New York: John Wiley. 257 p.

Grime, J.P. 1979. Plant strategies and vegetation processes. New York: John Wiley. 222 p.

Groombridge, B. 1992. Global biodiversity: status of the Earth's living resources. World Conservation Monitoring Centre. New York: Chapman and Hall. 585 p.

Hairston, N.G., Sr. 1989. Ecological experiments: purpose, design and execution. New York: Cambridge University Press. 370 p.

Hayek, L.C.; Buzas, M.A. 1997. Surveying natural populations. New York: Columbia University Press. 653 p.

Heywood, V.H., ed. 1995. Global biodiversity assessment. United Nations Environment Programme. New York: Cambridge University Press. 1,140 p.

Hilborn, R.; Mangel, M. 1996. The ecologic detective: confronting models with data. Princeton, NJ: Princeton University Press. 315 p.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton, NJ: Princeton University Press. 375 p.

Hunter, M.L. 1980. Microhabitat selection for singing and other behavior in great tits, *Parus major*: some visual and acoustical considerations. Animal Behavior. 28: 468–475.

Hunter, M.L. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Englewood Cliffs, NJ: Prentice Hall, Inc. 370 p.

Hurlbert, M.L., Jr., ed. 1999. Maintaining biodiversity in forest ecosystems. New York: Cambridge University Press. 698 p.

Husch, B.; Miller, C.I.; Beers, T.W. 1982. Forest mensuration. New York: John Wiley. 402 p.

Huston, M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge, MA: Cambridge University Press. 681 p.

Hynes, H.B.N. 1972. The ecology of running waters. Toronto, Canada: University of Toronto Press. 555 p.

Jaccard, P. 1912. The distribution of the flora of the alpine zone. New Phytologist. 11: 37–50.

Kimmins, J.P. 1997. Forest ecology: a foundation for sustainable management. Upper Saddle River, NJ: Prentice Hall; Simon and Schuster. 596 p.

Kingsland, S.E. 1985. Modeling nature: episodes in the history of population ecology. Chicago: The University of Chicago Press. 267 p.

Kohm, K.A.; Franklin, J.E., eds. 1997. Creating a forestry for the 21st century: the science of ecosystem management. Chicago: Island Press. 475 p.

Krebs, C.J. 1989. Ecological methodology. New York: Harper Collins Publishers, Inc. 654 p.

Langer, L.L.; Flather, C. 1994. Biological diversity: status and trends in the United States. Gen. Tech. Rep. RM–244. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 25 p.

LaRoe, E.T.; Farris, G.S.; Puckett, C.E. [and others], eds. 1995. Our living resources: a report to the Nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. Washington, DC: U.S. Department of the Interior, National Biological Service. 530 p.

Lloyd, M.; Ghelardi, R.J. 1964. A table for calculating the equitability component of species diversity. Journal of Animal Ecology. 33: 217–225.

Lubchenco, J.; Olsen, A.M.; Brubaker, L.B. [and others]. 1991. The sustainable biosphere initiative: an ecological research agenda. Ecology. 72: 371–412.

MacArthur, R.; Wilson, E.O. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press. 203 p.

Machlis, G.E.; Forester, D.J. 1996. The relationship between socio-economic factors and the loss of biodiversity: first efforts at theoretical and quantitative models. In: Szaro, R.C.; Johnston, D.W., eds. Biodiversity in managed landscapes. New York: Oxford University Press: 121–146.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton, NJ: Princeton University Press. 179 p.

Margalef, D.R. 1958. Information theory in ecology. General Systems Bulletin. 3: 36–71.

Maser, C. 1994. Sustainable forestry: philosophy, science, and economics. Delray Beach, FL: St. Lucie Press. 373 p.

McIntosh, R.P. 1985. The background of ecology: concept and theory. Cambridge, MA: Cambridge University Press. 383 p.

Monk, C.D. 1967. Tree species diversity in the eastern deciduous forest with particular reference to north central Florida. The American Naturalist. 101(918): 173–187.

Noss, R.F.; Cooperrider, A.Y. 1994. Saving nature's legacy: protecting and restoring biodiversity. Washington, DC: Island Press. 416 p.

Noss, R.F. 1996. Conservation of biodiversity at the landscape scale. In: Szaro, R.C.; Johnston, D.W., eds. Biodiversity in managed landscapes. New York: Oxford University Press: 574–589.

Odum, E.P. 1959. Fundamentals of ecology. Philadelphia: W.B. Saunders Co. 546 p.

Oliver, C.D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management. 3: 153–168.

Oosting, H.J. 1956. The study of plant communities. 2d ed. San Francisco: Freeman Publishing, Inc. 440 p.

Peet, R.K. 1974. The measurement of species diversity. Annual Review of Ecological Systematics. 5: 285–307.

Peet, R.K. 1975. Relative diversity indices. Ecology. 56: 496–498.

Perry, D.A. 1994. Forest ecosystems. Baltimore: The John Hopkins University Press. 649 p.

Pickett, S.T.A.; Ostfeld, R.S.; Shachak, M.; Likens, G.E., eds. 1997. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. New York: Chapman and Hall/ International Thompson. 466 p.

Pielou, E.C. 1969. An introduction to mathematical ecology. New York: John Wiley. 326 p.

Pielou, E.C. 1974. Population and community ecology. New York: Gordon and Breach. 424 p.

Pielou, E.C. 1975. Ecological diversity. New York: John Wiley. 165 p.

Pielou, E.C. 1977. Mathematical ecology. New York: John Wiley. 385 p.

Powell, D.S.; Faulkner, J.L.; Darr, D.R. [and others]. 1993. Forest resources of the United States, 1992. Gen. Tech. Rep. RM–234. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 132 p.

Powledge, F. 1998. Biodiversity at the crossroads. Bioscience. 48(5): 347–352.

Preston, F.W. 1948. The commonness and rarity of species. Ecology. 29: 254–283.

Reaka-Kudla, M.L.; Wilson, D.E.; Wilson, E.O., eds. 1997. Biodiversity. II. Washington, DC: Joseph Henry Press. 551 p.

Ricklefs, R.E.; Schluter, D., eds. 1993. Species diversity in ecological communities: historical and geographical perspectives. Chicago: University of Chicago Press. 414 p.

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge, MA: Cambridge University Press. 436 p.

Rosson, J.F., Jr. 1999. An analysis of the temporal dynamics in tree species diversity for major tree taxa of two States in the Midsouth, U.S.A. Knoxville, TN: University of Tennessee. 257 p. Ph.D. dissertation.

Rosson, J.F., Jr. 2001. Forest resources of Mississippi, 1994. Resour. Bull. SRS–61. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 78 p.

Salwasser, H.; MacCleery, D.W.; Snellgrove, T.A. 1992. New perspectives for managing the U.S. National Forest Systems. Report to the North American Forestry Commission, 16th Session. Cancun, Mexico: [Publisher unknown]. [Not paged].

Scheiner, S.M. 1993. Introduction: theories, hypotheses, and statistics. In: Scheiner, S.M.; Gurevitch, J., eds. Design and analysis of ecological experiments. New York: Chapman and Hall, Inc.: 1–13.

Schluter, D.; Ricklefs, R.E. 1993. Species diversity: an introduction to the problem. In: Ricklefs, R.E.; Schluter, D., eds. Species diversity in ecological communities: historical and geographic perspectives. Chicago: University of Chicago Press: 1–10.

Sites, J.W., Jr.; Crandall, K.A. 1997. Testing species boundaries in biodiversity studies. Conservation Biology. 11(6): 1289–1297.

Skov, F. 1997. Stand and neighbourhood parameters as determinants of plant species richness in a managed forest. Journal of Vegetation Science. 8(4): 573–578.

Smith, D.M. 1962. The practice of silviculture. New York: John Wiley. 578 p.

Smith, W.B.; Vissage, J.S.; Darr, D.R.; Sheffield, R.M. 2001. Forest resources of the United States, 1997. Gen. Tech. Rep. NC–219. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 190 p.

Sokal, R.R.; Rohlf, F.J. 1995. Biometry. San Francisco: W.H. Freeman and Co. 887 p.

Solomon, D.L. 1979. A comparative approach to species diversity. In: Grassle, J.F.; Patil, G.P.; Smith, W.K.; Taillie, C., eds. Ecological diversity in theory and practice. Fairland, MD: International Cooperative Publishing House: 29–35.

Stapanian, M.A.; Cassell, D.L.; Cline, S.P. 1997. Regional patterns of local diversity of trees: association with anthropogenic disturbance. Forest Ecology and Management. 93(1): 33–44.

Stein, B.A.; Kutner, L.S.; Adams, J.S., eds. 2000. Precious heritage: the status of biodiversity in the United States. New York: Oxford University Press. 399 p.

Szaro, R.C.; Johnston, D.W. 1996. Biodiversity in managed landscapes: theory and practice. New York: Oxford University Press. 778 p.

U.S. Environmental Protection Agency. 1990. Threats to biological diversity in the United States. PM–233X. Washington, DC: Office of Policy, Planning, and Evaluation. [Not paged].

Wallace, A.R. 1876. The geographical distribution of animals. New York: Hafner Publishing. 1,110 p. 2 vol.

Williams, C.B. 1944. Some applications of the logarithmic series and the index of diversity to ecological problems. Journal of Ecology. 32(1): 1–44.

Williams, C.B. 1953. The relative abundance of different species in a wild animal population. Journal of Animal Ecology. 22: 14–31.

Willis, J.C. 1922. Age and area: a study in geographical distribution and origin in species. Cambridge, MA: Cambridge University Press. 259 p.

Wilson, E.O.; Peter, F.A., eds. 1988. Biodiversity. Washington, DC: National Academy Press. 521 p.

Wolda, H.; Woodwell, G.M.; Smith, H.H., eds. 1969. Diversity and stability in ecological systems. Brookhaven symposium in biology, 22. Upton, NY: Atomic Energy Commission, Brookhaven National Laboratory. [Not paged].