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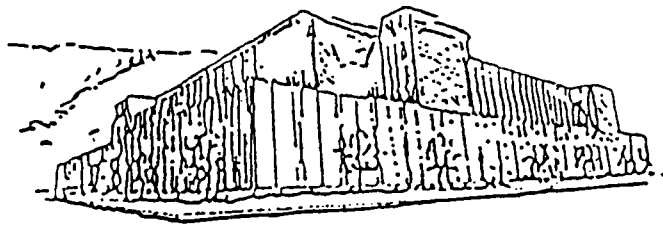
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*WETLAND VASCULAR PLANT COMMUNITY DIVERSITY
IN MONTANA*

by

Tom Parker

B.S. The University of Montana, 1988

Thesis

for partial fulfillment of requirements

for the degree of

Master of Science

The University of Montana

1996

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Wetland Vascular Plant Community Diversity in Montana

Director: Paul L. Hansen *PLH*

Land managers have asked the Montana Riparian and Wetland Association (MRWA) to help them understand how they can incorporate diversity when they develop management plans. The MRWA has developed an ecological type classification for Montana based on wetland vascular plant communities. Using data from 2,702 plots sampled to develop the classification, I calculated three measures of diversity—Shannon's index, Simpson's index and species richness—for each plot, and then examined the results to address two major questions: 1) What kind of information do the indices offer? and 2) Once that is known, how can the indices best be used to describe diversity differences among different ecological types?

I found that correlations between species richness and the two diversity indices decrease as plant communities become more complex. With simple plant communities like those dominated by grasses, it might be enough to use species richness by itself, while in more complex communities dominated by shrubs or trees, it can be useful to supplement species richness with either Shannon's index or Simpson's index. The indices were able to detect differences among ecological types when plots representing those types were grouped into tree, shrub or non-woody categories. However, the indices lost their discriminating power when comparing ecological types that are similar, or when comparing a small number of plots.

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INTRODUCTION

Recent legislation and policies direct land managers to include biodiversity as a management objective. The National Forest Management Act of 1976 requires National Forest managers to “provide for diversity of plant and animal communities...in order to meet overall multiple-use objectives” (USDA 1992). The Council on Environmental Quality (1993) recommended policies to incorporate biodiversity into Environmental Impact Analyses under the National Environmental Policy Act (NEPA). Proper Functioning Condition (PFC) guidelines for wetlands include biodiversity considerations (USDI 1993). E.O Wilson said, “There is no question in my mind that the most harmful part of ongoing environmental despoliation is the loss of biodiversity.” (Wilson and Kellert 1993).

These policies and this heartfelt statement all refer to biodiversity in very general terms. In order for land managers to plan for, or manage for biodiversity, they must be able to communicate about biodiversity with a specific, common language. They need tools to monitor biodiversity with respect to targets they specify. Finally, they must be able to quantify their objectives.

Raven (1994) states, “At the simplest level, biodiversity is the sum total of all the plants, animals, fungi and microorganisms in the world, or in a particular area; all of their individual variation; and all of the interactions between them.”

McMinn (1991) defines biodiversity as “...the diversity of life, including the diversity of genes, species, plant and animal communities, ecosystems, and the interaction of these elements.” The Council on Environmental Quality (1993)

notes, "Emerging concern about biodiversity reflects an empirically based recognition of the fundamental inter-connections within and among various levels of ecological organizations. Ecological organization, and therefore biodiversity, is a hierarchically arranged continuum, and reduction of diversity at any level will have effects at the other levels."

Biodiversity definitions all seem to capture three main elements. First, biodiversity refers to all living things in aggregate. Second, biodiversity refers to the variation among units of life as expressed by species, genera, and other human-imposed taxonomic divisions; and to the variation within units of life as expressed by genes. Finally, biodiversity includes the holistic idea that living units of variation are parts of a larger system with hierarchies of interactions expressed by energy flows.

The Importance of Wetlands and Riparian Areas

The Montana State University Extension Service (1994) lists several benefits that come from maintaining a healthy riparian area. Wildlife use riparian corridors for travel, cover and as a source for browse and grazing forage. Healthy riparian areas filter sediment and release water late into the summer season, providing clean water. Between one and five percent of land area is in riparian areas, but 75% of species live and grow there. Overhanging trees and shrubs provide shade for fish. Plant parts that fall into streams provide basic food for stream insects, which then provide food for fish. Deep, fertile, moist soils allow trees to grow faster than in adjacent upland sites.

A fully vegetated riparian area buffers the effects of floods by slowing water and trapping sediment that is transported during high flow events. This trapped sediment then provides a soil substrate that allows plants' seeds to germinate. Deep-rooted trees, shrubs and graminoid species hold banks together, further buffering the stream from the effects of high water. Riparian areas are usually pleasant places for people, for many of the same reasons that wildlife and plants tend to congregate there. Riparian areas allow recreational activities like fishing, boating and bird watching. Often, floodplains along riparian areas offer the only flat place to put a trail, highway, gas pipeline or railroad in mountainous country. Many ranches and homes are located along riparian corridors.

Hansen and others (1995) say wetlands

“are of prime importance to water quality, water quantity, stream stability, and fisheries habitat. They are vital to the livestock grazing industry and many are also well suited for development as high quality agricultural farmland. In addition, many riparian or wetland sites are excellent timber producing sites. Most sites provide critical habitat needs for many species and they support a greater concentration of wildlife species and activities than any other type of location on the landscape. In addition, riparian or wetland areas can be considered the ‘threads’ that tie together all the other ecosystems.”

Plant community diversity forms the template for many of these wetland functions. Peat building, sediment trapping, nutrient retention, water shading, and transpiration all depend on plants' unique morphologies and physiologies. Plant communities' species composition influences their function. Peat bogs derived from mosses are less permeable than those that develop from decaying grasses and sedges (Mitsch and Gosselink, 1993). Spruce roots grow near the surface and create sturdy, overhanging banks that provide shelter for fish.

Water, directly and indirectly, controls wetland species composition and distribution. Anaerobic soil limits the number of species that can grow in a stillwater wetland. Even fewer plant species can grow in standing water. Water moving through soil oxygenates the soil, allowing species with a wider range of adaptations to occupy the site. Transported and deposited sediments create subtle topographic relief (spatial heterogeneity). Resulting subtle differences in soil permeability and oxygen content create varied microsites, and resulting variation in plant communities (Mitsch and Gosselink 1993).

Purpose and Goals of the Study

In May, 1995, Hansen and others with the Montana Riparian and Wetland Association (MRWA) completed *Classification and Management of Montana's Riparian and Wetland Sites*. This document is a vegetation-based classification that describes 113 ecological types found throughout Montana. For each type, complete vascular plant species lists accompany descriptions of plant ecology, soils, hydrology, land forms, and adjacent plant communities. General management recommendations address fire, wildlife, recreation, livestock and soils. While developing the classification, the authors did not address biodiversity directly. After the document was nearly completed, Paul Hansen, one of the authors, decided that data used to create the classification might also be used to characterize biodiversity. Land managers in Montana had expressed uncertainty about how biodiversity might apply to managing their riparian areas and other wetlands.

In response to this question posed by land managers, I investigated biodiversity in the light of a data set which has already been interpreted based on component

species' known ecologies. For example, if a plant community dominated by sedges is known to stabilize soil better than one dominated by an annual grass, does that mean the sedge community is more diverse? A simplified notion of biodiversity might lead us to expect a more stable community to have *more* biodiversity. But it is difficult to isolate what we mean by more biodiversity. To remedy this, biologists talk about diversity instead of biodiversity. Magurran (1988) points out that at first glance diversity appears easy to understand since it is a common word unlike many words ecologists use. Diversity is in fact an unexpectedly complex concept that has spawned considerable controversy. This is because diversity has two components—variety and relative abundance (richness and evenness). Ecologists have developed vast and complicated ways to quantify this dual concept. Magurran (1988) and Tokeshi (1993) provide excellent summaries and critiques of many diversity indices that have been developed since the 1940's. This array of possibilities led to my goals for this study: 1) determine what signals some commonly used measures of diversity provide in light of the large data set assembled by MRWA as they built their classification; and 2) determine whether these diversity indices are useful tools for describing differences among Montana's wetland sites.

To develop their classification, MRWA staff sampled nearly 3,000 plots located in riparian and other wetland areas throughout Montana. At each plot, the researcher identified all species present and recorded their canopy cover. Canopy cover is the proportion of ground in a plot that would be blocked by a species if the plot was viewed from above. These data are useful for describing alpha diversity, which is a combination of richness and evenness within a collection (Magurran 1988). Here, a collection includes all vascular plant species found

within a 50m² plot (375m² for tree-dominated plots). Richness is the number of species recorded in a plot, and evenness refers to how abundant each species is relative to the other species in a plot. In addition to alpha diversity, ecologists recognize three other major diversity scales: beta (between-habitat); gamma (landscape); and epsilon (regional) diversity. Refer to Chapter 2 for a discussion of these different scales.

In this study, I focused on alpha diversity, so I will refer to alpha diversity as simply *diversity*. I calculated three diversity indices for each of 2,702 plots. The first, species richness, is simply a count of species within a plot and is not a true diversity index since it ignores evenness. The other two, Shannon's index and Simpson's index are similar because they sum all species' proportional abundance in a plot. Shannon's index is considered to be more sensitive to less abundant (rare) species, while Simpson's index is considered to be more sensitive to dominant species (Peet, 1974). I calculated these indices for two reasons. First, I wanted to see if the indices worked as advertised when placed under the bright light of 2,702 biological collections (plots). Then, after learning how the indices respond to differences in plant community structure, I used them to sort out differences in diversity among the ecological types described in *Classification and Management of Montana's Riparian and Wetland Sites* (Hansen and others 1995).

While building this classification, the authors assumed that wetland plant communities are discrete enough that different people can use the same dichotomous key independently and classify a patch of forest, shrubland or meadow into the same one of 113 possible ecological types. MRWA field crews

have repeatedly shown this to be true (personal observation). Within the classification, ecological types can be either habitat types or community types. Habitat types follow a relatively predictable sequence of successional stages that end in a potential natural community, which is sometimes referred to as a climax community. Community types seldom reach a potential natural community because they are located in areas dominated by natural disturbances such as frequent floods, or by human-caused disturbances such as prolonged heavy livestock grazing. Groups of plots that were classified as habitat types are separated into two seral or developmental stages: early or mid seral; and late seral or climax. The remaining plots that were classified as community types were separated into disturbed or undisturbed plots depending on the amount of human-caused disturbance evidenced on a site.

Plots were thus classified as one of 113 ecological types, and then further divided by their seral stage or by disturbance categories. Based on the vegetation in their tallest vertical layer, ecological types fall into six life form groups: conifers; deciduous trees; willows; other shrubs; sedges; and other herbaceous plants. I used all of these categories to test how sensitive the diversity indices are at different scales. More specifically, I compared diversities among several ecological types, among different life forms, between seral stages or disturbance categories, and with combinations of these different groupings. For some comparisons, I lumped conifers and deciduous trees into a tree category, willows and other shrubs into a shrub category, and sedges and other herbaceous plants into an herbaceous plant category.

I devoted one chapter to the concept of ecological diversity, while in another chapter I reviewed knowledge about the relationship between wetland ecology and plant community diversity. Using a data set that includes vascular plant species and their associated canopy covers from 2,702 sampled plots located in Montana, I built a local context for understanding how the theories of ecological diversity apply to real plant communities. Finally, I discussed how land managers can apply this knowledge to managing Montana's wetland plant communities.

THE DIVERSITY CONCEPT

Diversity is a combination of richness and evenness. Richness is simply the number of species (or other units) counted in a sampled plot, while evenness is the relative abundance of those species sampled within the plot (Magurran 1988). Throughout this study, I use “canopy cover” to quantify abundance. For example, if a plot has ten species, and one of those species clearly dominates, that plot will have a lower evenness than a plot with 10 species that are equally abundant in terms of canopy cover. Since diversity combines richness and evenness in its strict ecological definition, people developing diversity indices have tried to reflect both aspects in one index.

Peet (1974) recognized three conceptual approaches to diversity: species richness; heterogeneity; and equitability. Species richness is an estimate of the number of species present in an area. By using “species richness” instead of “species number,” allowance is made for sampling limitations since a researcher may fail to record one or more species that is present. As a concept, species richness represents the number of species without actually being the true number. Peet (1974) remarks, “Direct species counts, while lacking theoretical elegance, provide one of the simplest, most practical, and most objective measures of species richness.” In other words, the best way to find out how many species are out there is to count them. Describing heterogeneity, Peet recognized that two samples with the same number of species have different diversities if the species’ relative abundances are different between the two samples. Thus, heterogeneity combines richness and evenness. Given two collections that are equally rich, Peet would say that the collection whose species are more evenly distributed in terms

of their relative abundance is more diverse. Equitability ignores richness and focuses solely on how evenly distributed species are in terms of their relative abundance. By using the terms richness, heterogeneity, and equitability, Peet was really describing richness, diversity, and evenness. Ecologists have tended to use the latter three terms, but they often parenthetically mix in the former.

Based on spatial scales, ecologists have defined different levels of diversity (Whittaker 1965 and Magurran 1988). These are point diversity, alpha diversity, beta diversity, gamma diversity and epsilon diversity. Point diversity is the diversity of a sample taken from within a sampled plot. Alpha diversity is the diversity that describes a habitat class, and this is arrived at by averaging point diversity from within several plots that represent a particular habitat class (Hurlbert 1971). For example, 32 plots sampled by the MRWA fell into the *Agropyron smithii* (western wheatgrass) habitat type. When I calculated diversity for each of these 32 plots individually, I was working at the point diversity scale. When I averaged these, I was estimating alpha diversity for the *Agropyron smithii* (western wheatgrass) habitat type. In this study, I did not go beyond alpha diversity, but I do recognize that land managers may benefit by considering larger scales. Beta diversity describes the change in diversity between adjacent habitats and along environmental gradients. Similarity indices are one common method to quantify beta diversity. Gamma diversity describes the diversity of a group of alpha diversities across a landscape. Finally, epsilon diversity describes regional diversity, or the diversity of gamma diversities (Magurran 1988).

Confusion About the Meaning and Usefulness of Diversity

Hurlbert (1971) criticized the concept of diversity as it was being applied to ecology by his contemporaries, calling it a “non-concept.” He insisted that diversity’s definition be restricted to “the number of species present (species richness or species abundance) and the evenness with which the individuals are distributed among these species (species evenness or species equitability).”

Hurlbert believed that in order to be meaningful, diversity must contain both these components, and cannot denote richness or evenness and exclude the other. Hurlbert traces diversity indices’ creation to a gut feeling among ecologists that number of species and their relative abundances could be combined into a single, useful measure. In addition to insisting that diversity’s definition be limited to richness and evenness, Hurlbert cautioned biologists against using mathematical diversity measures to interpret natural systems.

McIntosh (1967) notes that diversity has been said to “increase in a successional sequence to a maximum at climax, to enhance community stability, and to relate to community productivity, integration, evolution, niche structure, and competition...Measurements of community properties such as diversity, stability, or productivity are enlightening only when the entity in which they are made is meaningful.” The MRWA’s classification uses habitat types (and community types) as these entities. Daubenmire (1968) defines habitat types as “all the area (sum of discrete units) that now supports, or within recent time has supported, and presumably is still capable of supporting, one plant association... .” When developing a habitat type, one assumes that different plant associations capture a reasonable amount of the abiotic variation on a landscape. In this study, I heeded Hurlbert’s caution by carefully investigating how my chosen diversity indices

react and by comparing these reactions to our knowledge of the various habitat types and community types.

Pielou (1966) pointed out that different types of collections require different methods for determining their diversity. Plant communities fall into her type “E” class of collections, because they must be “examined in situ” and they have a patchy spatial pattern. Random sampling will overlook species and underestimate the number of species present in an area. Since MRWA researchers sampled within patches—for example, patches of shrubs or sedge meadows—avoiding edges and slight topographic irregularities, they reduced the amount of variation in their samples that might have come from different environmental conditions.

Evaluation of Some Diversity Indices

Peet (1974) says

“Diversity, in essence, has always been defined by the indices used to measure it, and this has not fostered the sort of uniformity which allows the clear statement of ideas and hypotheses. Progress in ecology, as in all science, depends upon precise and unambiguous definition of terms and concepts.”

In his often-cited synthesis paper on species diversity measurement, Peet attempts to “...define in a precise but still generalized manner, what is or should be meant by the many terms surrounding the concept-cluster diversity.” Peet succeeded somewhat in standardizing diversity index definitions and applications. He did this in a “generalized” manner, but failed to achieve the precision of definition he sought. As Hurlbert suggested, diversity measures, in

order to have precise meaning, must be understood in terms of a real ecological system and the particular species relationships in that system.

Diversity indices are often discussed in the literature and compared to ideal data sets with a large number of species. The Q-statistic, which is based on the inter-quartile slope of the species abundance distribution, was proposed by Lamont and others (1978), and recommended by several researchers as more useful than the traditional Simpson and Shannon indices (Kempton and Wedderburn 1978; Magurran 1988):

$$Q = \frac{1/2S}{\log_e R_2 - \log_e R_1} \quad (1)$$

where S is the total number of species in a sample and where R₂ and R₁ are the upper and lower quartiles respectively in a ranked list of species' canopy covers.

However, since wetland plant communities often contain very few species (sometimes as few as one), calculation of diversity statistics that depend on an abundance distribution without definite quartiles is difficult and probably meaningless. Tokeshi (1993) brings up this point and proposes a synthesis of several community structure models. His approach may be more useful, and would be worth testing on plant communities with larger species lists. However, because wetland vascular plant communities often contain so few species, I did not test the Q statistic or any others that rely on these quartiles. Instead, I chose

Shannon's index and Simpson's index because they take into account relative abundance for all species that are present.

Hill (1973) proposed that Shannon's index and Simpson's index unify the concepts of richness and evenness into one concept—diversity. Routledge (1979), calling them Hill's family of indices, claims that they are the only admissible indices. Routledge lists several criteria for an admissible diversity index. First, the index "ought to be a function of the proportional abundances of the species." Proportional abundance is the proportion of the total canopy cover of all species in a plot that each species represents. Total canopy cover can be greater than 100% since species overlap each other in vertical layers, so canopy cover alone is not necessarily "proportional abundance." The index must also be able to extend across taxonomic hierarchies. For example, the index would somehow recognize that a plant family with fewer genera and species represented in a sample contributes more to diversity than does a plant family with more genera and species. Pielou (1975) describes a method to evaluate taxonomic hierarchical diversity based on Shannon's index. Few studies have considered taxonomic hierarchy, however; most use species as the sole unit of taxonomic differentiation. I restricted this study to species diversity, since the classification is based on species. Still, I do not discount the potential for using families and genera, or perhaps other categories that may be important to a particular investigation.

I selected Shannon's index, Simpson's index and species richness for this study, and the formulas follow:

Species Richness

Species richness is the number of species counted in a sample.

Shannon's Index

$$\text{Shannon's index } (H') = -\sum_{i=1}^S p_i \ln(p_i) \quad (2)$$

where S = # of species and
 where p_i = proportional abundance of species_{*i*} (cover of species_{*i*} / total cover of all species in sample).

Simpson's Index

$$\text{Simpson's index } (D) = \sum_{i=1}^S p_i^2 \quad (3)$$

where S = # of species and
 where p_i = proportional abundance of species_{*i*} (cover of species_{*i*} / total cover of all species in sample).

Since D decreases as diversity increases, Simpson's index is usually expressed as $1/D$ or $1-D$ (Magurran 1988). I used $1-D$ so that Simpson's index will increase with Shannon's index. It is interesting to note that Hurlbert (1971) used $1/D$ when he illustrated that Simpson's index does not necessarily increase with Shannon's index. That example was the basis for his argument that diversity indices are often contradictory. Although he did not publish his raw data, I suspect that using $1-D$ would invalidate that argument.

Both Simpson's and Shannon's indices increase with the number of species (richness) and how evenly those species are spread throughout a stand

(evenness). Because of this, they potentially offer more information than species richness alone. Shannon's index tends to be affected more by rare species (diversity's richness component), while Simpson's index tends to be more affected by changes in the abundance of the most dominant species (Peet 1974).

Simpson's index (D), according to Peet (1974), measures the probability that two individuals selected at random from a sample will belong to the same species. Subtracting D from one causes Simpson's index to increase as richness and evenness increase. Hurlbert's (1971) probability of interspecific encounter (PIE), which is $1/D$, is a form of Simpson's index. The reciprocal of D can be interpreted as "the number of equally common species required to produce the same heterogeneity as observed in the sample (Peet 1974)." Simpson's, as a Type II index according to Peet (1974) is most sensitive to changes in the importance of the most abundant species. Formally, with Simpson's index, the second derivative's absolute value decreases or remains constant as species abundance approaches zero.

Shannon's index (H') has been referred to in the literature alternately as the "information theory index," "Shannon-Weaver," and "Shannon-Wiener." Each of these names refers to the same index. Shannon's index relates diversity to the amount of uncertainty associated with a randomly selected individual drawn from a population. Peet (1974) labels Shannon's index a Type I heterogeneity index because it is most sensitive to changes in the rarest species. Formally, the second derivative's absolute value increases as species abundance approaches zero. For example, Peet says "The effect of a change of 0.01 importance for a pair of species with initial importances of 0.01 and 0.5 will be greater for the rarer

species." Conversely, a change in the more abundant species would cause a greater change in Simpson's index.

Much of the debate centers around defining the statistical properties of these indices literally in terms of probabilities of species encountering each other. Hurlbert (1971) seems somewhat favorable toward this view, as it agrees with his insistence on defining diversity in terms of its biological meaning. His probabilities of interspecific encounter (PIE), a conceptual model that he quantifies using a form of Simpson's index, could imply a certain level of ecological complexity, where high PIE drives ecological interactions which yield, according to Hurlbert, ecological stability. Particularly in the case of plant communities, a PIE-driven concept of diversity is limiting, since the plants themselves cannot freely encounter each other in the same way that animals can. In the case of plant communities, diversity indices are probably more useful for explaining community structure than ecological processes.

Hill (1973) summarized previous authors' views as, "diversity is essentially a structural concept" and cannot be separated from theories of community organization. He points out that, "Diversities are mere numbers and should be distinguished from the theories which they support." Diversity is a measurable parameter whose observed values can be correlated to "stability, maturity, productivity, evolutionary time, predation pressure, and spatial heterogeneity." His point seems to be that diversity measures can be explained by these different phenomena, but that the measures are independent of these theories. Based on this idea, it makes the most sense to proceed as follows: 1) understand an ecological system by reviewing literature and observing the system;

2) investigate how diversity indices respond based on this knowledge; and 3) use this information to interpret values of diversity indices that come from this particular system.

ECOLOGY OF WETLAND PLANTS AS IT RELATES TO COMMUNITY DIVERSITY

By reviewing the following literature, I begin to extract theories about wetland plant community organization that can help explain community diversity trends revealed by analyzing plot data from the classification data set. My analysis of the data will also allow me to develop hypotheses to explain trends not addressed in the literature. Increasingly, managers are being required to set biodiversity as an objective. Since biodiversity is a broad concept, I use diversity as a quantifiable surrogate. With that in mind, this review broadens the base upon which we can build an understanding of what diversity indices really mean ecologically, and how they can help us set management objectives and then monitor those objectives.

For wetlands to be legal (jurisdictional) wetlands, they need to have wetland hydrology, wetland vegetation and wetland soils. Scientists tend to use a functional definition for wetlands; by this definition, an area needs to have only one of the three above criteria (Army Corps of Engineers 1987).

While wetland vegetation and soils remain relatively constant, at least over a short time frame, wetland hydrology varies spatially between different “wetlands” and over time in the same wetland. Wetland plant ecologists have recognized two main classes of wetland hydrologic regimes that affect plant communities in very different ways. Some wetlands have surface water throughout most of the year, so their hydrology is characterized by constant flooding. Other wetlands are flooded during part of the year, and dry during the

remainder of the year. Using these two classes, ecologists have noted different plant forms and physiological strategies. Flooded wetland plant communities' composition and structure is driven more by biotic factors, while seasonally flooded wetlands' composition and structure is driven more by abiotic factors (Mitsch and Gosselink 1993).

Biotic Controls in Areas with Less Variable Hydrology

Breen and others (1988) describe swamps as permanently flooded areas where hydrologic conditions are relatively constant. These constant conditions allow longer-lived plants to colonize a given habitat. Reproductive strategies are mostly vegetative, due to the lack of seed germination substrate. These plant communities tend to contain clonal clumps of tall, fibrous, perennial herbaceous species with well-developed rhizomatous root systems. Thick, rhizomatous below-ground mats tend to monopolize rooting substrate leading to monospecific groupings and a low species diversity. Ingram (1967) suggested that plant growth in anaerobic, waterlogged soils is not affected as much by the lack of oxygen, but by anoxia's indirect effects. These indirect effects include microbial activity, solubility of toxic metal ions, and high concentrations of CO₂ and sulfur dioxide.

Braendle and Crawford (1987) found that rhizomes exhibited a wider tolerance range to anaerobic conditions than do traditional roots in swamp species. Air spaces in plant tissues (either aerenchyma or hollow internodes) served to provide oxygen to below ground living tissue. These air spaces also allowed for expulsion of the toxic byproducts of anaerobic metabolism, which may be an equally important adaptive mechanism. Bonasera and others (1979) examined

the potential for allelopathy in four marsh species. *Typha* spp. (cattail) leaf extracts inhibited growth of some bioassay species, although the bioassays were not native species typically found with cattails.

Breen and others (1988) argue that since plants modify their abiotic environment—for example, by slowing water and trapping silts—a particular species plays an active role in isolating itself from other species by creating conditions where only the former species can survive. Breen and others (1988) present this situation as a self-regulating (cybernetic) system. In a swamp, although high stress conditions limit productivity and species diversity (no direct tie is made here), energy inputs are slower but constant, with much energy being stored in slowly and seasonally released mineral forms in the soil. These systems, while having a low species diversity have high structural diversity. Bernard and Solsky (1977) studied a New York *Carex* spp. (sedge) community and recorded three main structural layers. The top layer (in autumn) consisted of one year old, dying shoots. The second layer was made up of 3-4 month old shoots of mixed height, and the third layer consisted of shorter, living shoots that would remain green over the winter. Some (N,P,K) nutrients were translocated to rhizomes, some remained above ground in living tissue. Ca and Mg were not stored in tissues. This multilayered strategy poised the *Carex* spp. (sedge) species for quick growth by allowing it to uptake nutrients in the spring.

While these studies have addressed specific plant species, they point to a host of strategies where wetland plants, once established, can retain their spatial position. In this environment it seems that whichever species establishes itself first can stay for a long time, as long as the hydrologic regime remains stable. By

limiting light to any exposed germination substrate, using all available resources, and forming a dense rhizomatous mat, these plants can assure themselves a resource monopoly on individual sites.

Johnson and others (1985) looked at abiotic and biotic factors in a successional sequence in the Mississippi River delta. They too concluded that hydrology drives processes that determine vegetation establishment. Floods lead to sedimentation, which leads to spatial or habitat heterogeneity. Once a very slightly elevated landform develops, *Sagittaria* spp. (an herb) can become established. When flooded, it dies back to tubers, and then emerges when floods recede. Its roots hold soil together and trap more sediment, allowing *Salix nigra* (black willow) to become established. Once the willow is established, its flexible, fibrous roots and stems buffer flood effects. *Typha* spp. (cattail) cannot withstand great water volumes and velocities, but will grow behind *Salix* spp. (willow) once the willow has developed enough to absorb some of the flood energy. Here, the abiotic environment creates initial conditions for vegetation, but then vegetation further modifies (or stabilizes) the environment to allow further development of the plant community.

Abiotic Controls in Areas with Variable Hydrology

Johnson and others (1987) examined zonation around glacial prairie marshes, noting that visual discreteness in plant communities is not always borne out by objective ordination analysis along a gradient. They found that presence or absence of highly visible species caused the human eye to draw lines where they may not really exist. However, they noted two distinct vegetation transitions that were correlated with abrupt changes in environmental conditions. Marsh and

meadow vegetation were separated by the main hydrologic regimes described above: constant flooding and period flooding. In this specific case, they hypothesized that wave action and ice scouring stressed marsh plants, limiting this zone's potential plant species composition. Meadow plants were not subjected to these stresses, but were subjected to variations in depth to the water table. Meadow to upland transitions were correlated with abrupt change in slope, perhaps reflecting historic water extents. In this work, they did not investigate or hypothesize about biotic controls for community composition; but other studies focus on plants' unique traits that allow them to survive and thrive under variable conditions.

Plant Traits as an Explanation for Community Structure and Composition

Some authors have separated plants by their life strategies in order to explain their distribution along gradients. Grime (1977) identified three plant types based on their strategies: stress-tolerators, ruderals, and competitors. Menges and Waller (1983) relate these to wetlands in terms of flood plain elevation and light gradients. Stress tolerators—for example sedges—survive floods or grazing by investing energy in substantial rhizomes and keeping their meristematic tissue (and therefore resprouting potential) at or below ground level. Grasses have similar resprouting ability. Ruderals (mostly annuals) can grow in areas that are less frequently flooded than stress tolerators. They grow quickly, taking advantage of post-flood nutrients and available water, then complete their life cycles before stresses again enter the picture. Competitors grow beyond the disturbance or flood zone, and usually have more biomass and perennial life cycles.

Menges and Waller (1983) point out that flooding regimes truly disturb only species that cannot tolerate floods. This invokes Odum's (1969) idea of pulse stability, where a system is stable relative to its adaptation to variation in abiotic factors. In North Dakota riparian wetlands, Johnson and others (1976) suggested that river meanders create a cycle of disturbance that maintains cottonwood and willow communities. These species depend on bare gravel substrate for germination. When these disturbance cycles are disrupted, alpha (within-habitat) diversity may increase as communities move toward climax, but gamma (landscape) diversity will decrease as fewer seral stages are represented in a given area.

Van der Valk (1981) chose different traits with which to separate plant life strategies. These were life-span, propagule longevity and propagule requirements. Life span's impact follows Menges and Waller (1983), but seed characteristics suggest a more biotic influence on which plants can colonize a site after abiotic variation causes changes in site conditions. Long-lived seeds wait for the right conditions for germination, while short-lived seeds germinate only when seed dispersal and adequate abiotic conditions coincide. Here, species' historic presence and their abundance outside the community can play a role in plant community composition. Van der Valk (1981) offers this concept as a qualitative null model useful for finding alternative (plant interaction) explanations for plant community composition and structure.

Breen and others (1988) describe a "zone of periodic inundation" where vegetation is zoned by the degree of exposure to variations in light, temperature,

nutrients and floods. Where floods are separated by long periods of dryness, annual grasses take advantage of the short window of growth opportunity. Some frequently flooded areas have plants with hollow stolons. These allow oxygen to get to roots during floods, and also allow rapid spreading of plants when flood waters recede and expose rich soil substrates.

Busch and Smith (1993) found that *Tamarix chinensis* (saltcedar)'s higher water use efficiency after fire made it a better post-disturbance competitor along southwestern river banks that exhibit periodic dry spells. *Salix* spp. (willow) and *Populus* spp. (cottonwood) had poor water use efficiency in comparison to *Tamarix chinensis* (saltcedar). They were also less able to quickly resprout than the non-native *Tamarix chinensis* (saltcedar).

Conclusion

Mitsch and Gosselink (1993) point out that although early wetland successional models predicted the shift from wetland to terrestrial, "there appear to be few, if any, examples of wetland ecosystems that became terrestrial without a concurrent allogenic lowering of the water level." In a sense, this goes back to the idea that wetlands are wet. Once you remove the water they will no longer be wetlands. More subtly, the structure and composition of vegetative communities in wetlands seems to be determined by when the wetlands are wet, and by how wet they are. Variation in hydrology as driven by geomorphology provides a template upon which biotic community development processes can happen. Wetland plants' strategies determine where they can grow in relation to this template, but these strategies also determine when they will be most abundant in a particular community.

People who use aspects of community ecology to aid in natural resources management seek ecologically based patterns to explain variation in plant communities on the landscape. Keddy and others (1994) use functional guilds, as expressed by morphological traits, to classify plants. As we seek methods for quantifying diversity, these functional classes may provide a more discriminating unit than species for explaining variation within and among plant communities in wetlands. However, since this study focuses on species to reflect the way *Classification and Management of Montana's Riparian and Wetland Sites* (Hansen and others 1995) is organized, we can still use species to quantify alpha diversity. If we then look at trends in alpha diversity based on ecological types' location in a wetland system, or along a successional gradient, we are in a sense creating functional classes. For example, ecological types in or very near water will probably have fewer species since fewer species have adapted to surviving in anaerobic conditions. At the other extreme, riparian coniferous forests often occur on slopes along straighter streams in mountainous country where the soil is well-oxygenated. Since oxygen is available, more species can grow, and overbank flows may not reach very high up a steep slope, thus limiting disturbance from floods. Here, then, is a possible context for interpreting diversity indices. This is also one justification for research whose goal would be to define correlations between water table depth and duration, and vascular plant species diversity in specific ecological types.

OBJECTIVES

In this study, I set the following goals: 1) determine what signals some commonly used measures of diversity provide in light of the large data set assembled by MRWA as they built their classification; and 2) determine whether these diversity indices are useful tools for describing differences among Montana's wetland sites. In order to meet these goals, I pursued the following objectives:

1. Examine correlations among three diversity indices to determine whether they are redundant, whether they are complementary, or whether the correlations vary depending on how plots are grouped.
2. Determine which diversity indices detect differences among plot groupings, and offer explanations for these results.
3. Present average diversity values for the different groupings.
4. Suggest tools that land managers can use to incorporate diversity into land management planning.

METHODS

Correlations Among Diversity Indices

I used Spearman's rank correlation coefficient (Noether 1991) to test for correlation between values calculated using different indices. Spearman's formula is:

$$r_s = 1 - \frac{6T}{n(n^2-1)} \quad (6)$$

n

where $T = \sum_{i=1}^n (R_i - S_i)^2$;

i=1

where R_i and S_i are rankings of the i^{th} plot according to two different indices; and where n = the number of plots.

Describing Plant Community Diversity with Selected Indices

As discussed earlier, both Shannon's index and Simpson's index have been evaluated for their mathematical properties by many authors. I calculated values for Shannon's and Simpson's index for all 2,702 sampled plots using FileMaker Pro 3.0, a commercial relational database from Claris Corporation. I used two statistical tests, Kruskal-Wallis (Noether 1991) and Kolmogorov-Smirnov (Steel and Torrie 1980), to determine whether differences among diversity index values for plots were significant when the plots were grouped by life form or by seral

stage. The Kruskal-Wallis test is a nonparametric completely randomized analysis of variance, and I used this test when identifying which groupings best explained variation in the diversity indices. I used the Kolmogorov-Smirnov two-sample test to determine whether groups of diversity index results came from the same population distribution.

Early tests convinced me that using species richness together with either Simpson's index or Shannon's index can provide more information than one index by itself. This also suggests that using an index like Shannon's by itself can lead to difficulties in interpreting results since this interpretation depends on species richness. Test runs using the Kolmogorov-Smirnov two sample test (Steel and Torrie 1980) showed that a single diversity index can discriminate between different plant communities. Interpreting what this discrimination means in the case of Shannon's index or Simpson's index may be difficult, however. The most effective method to identify which aspect (richness or evenness) of the two diversity indices determined their magnitude was to plot these indices against species richness and directly display that relationship. Figure 1 displays the relationship between Shannon's index and species richness for all plots that keyed into sedge-dominated ecological types. Relative abundance graphs, which rank species from highest canopy cover to lowest canopy cover along the x-axis, are another tool that is useful for interpreting these graphs (Fig. 2). Canopy cover is placed on the y-axis (Tokeshi 1993). A relative abundance graph visually represents a plant community's structure and supplements information given by diversity indices.

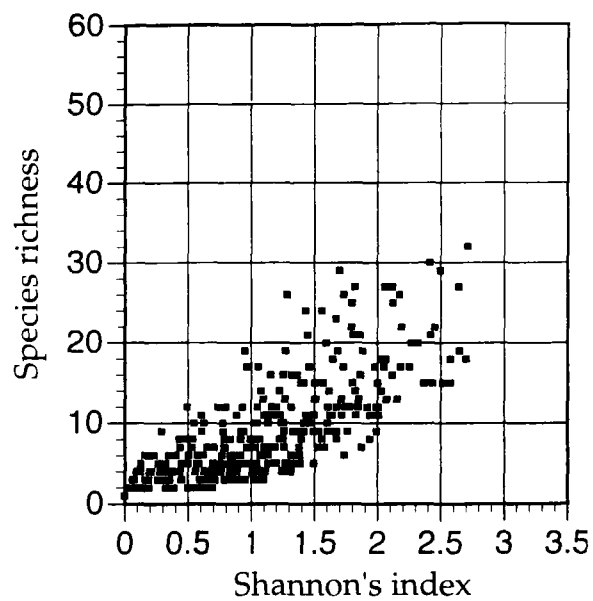


Figure 1. Species richness plotted against Shannon's index for sedge plots

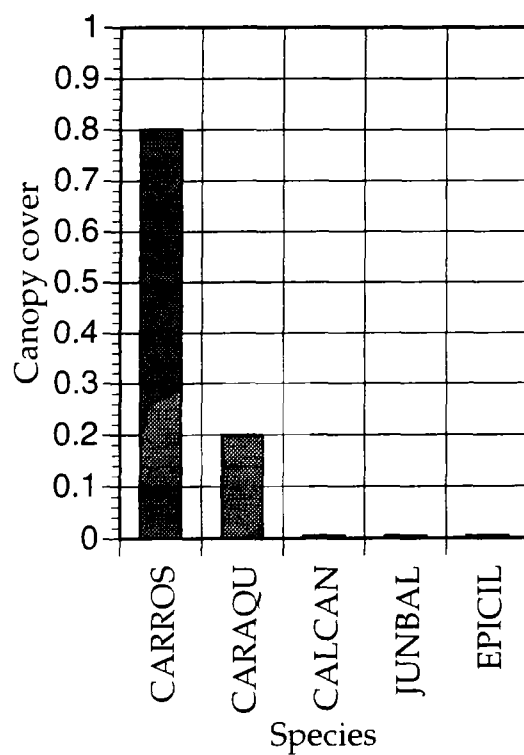


Figure 2. Relative abundance graph of a sedge plot

Sources of Variation

The main source of variation in this study is the difference in the plot size between sampled plots containing trees (375 square meters) and plots containing graminoids, forbs and shrubs (50 square meters). As sample area increases, the number of species (species richness) found in the sample tend to increase (Magurran 1988). Therefore, comparisons between tree-dominated plant communities and other plant communities contain a possible bias.

Another source of variation is sampling location. Plots that fall into the same ecological type were sampled from different regions in Montana. Using the Kruskal-Wallis (Noether 1991) one-way analysis of variance I found no difference in diversity index values within the same ecological type when plots were sampled in different parts of Montana.

Assumptions

I assume that all sampled plots were within homogeneous plant communities. Plant species are the units of information from which diversities are calculated. Sub-species or varieties of species are all treated equally as that species. Diversities are not normally distributed unless otherwise specified; for example, Shannon's index seems to be normally distributed in larger samples. All plant communities are treated the same regardless of their geographic locations in Montana.

RESULTS

The Nature of the Diversity Indices

For a given species richness, there is an upper and lower limit for Shannon's index or Simpson's index (Fig. 3). Shannon's index and Simpson's index are thus more meaningful when considered together with species richness. In order to illustrate this concept, I have analyzed the relationship between Shannon's index and species richness with respect to one plant community, the *Carex aquatilis* (water sedge) phase of the *Carex rostrata* (beaked sedge) habitat type. While one number (ex. Shannon=0.59) does not describe the structure of a plant community, this number, when combined with species richness, can paint a very broad picture of what that community looks like in a relative sense.

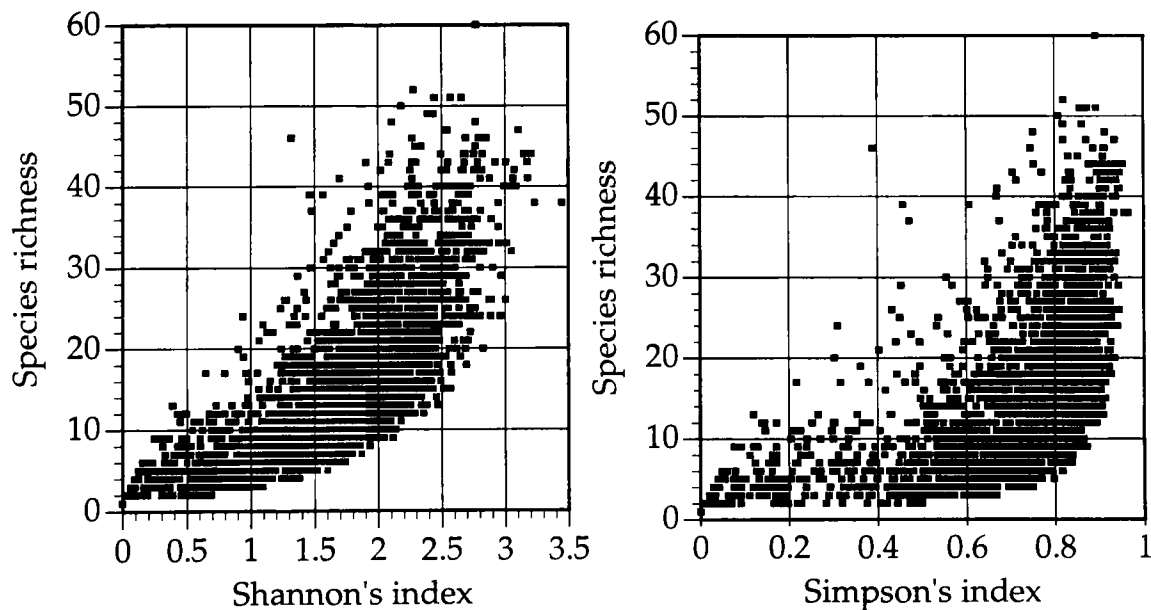


Figure 3. Relationship between Shannon's index and species richness (left) and Simpson's index and species richness (right) for 2,702 plots

A more useful quantitative measure of alpha diversity may be (species richness $[S]=5$, Shannon's index $[H']=0.59$) which denotes a plant community with five

species that is dominated by one or two species (indicated by a relatively low Shannon index of 0.59), and contains other species that are present in only trace amounts. On the other hand, ($S=5$, $H'=1.38$) describes a plant community with five species that are nearly equally abundant. Two relative abundance graphs (Fig. 4) illustrate the difference between these communities. Combining these numbers with a habitat type and seral stage, for example *Carex aquatilis* (water sedge) phase of the *Carex rostrata* (beaked sedge) habitat type, early/mid seral stage ($S=5$, $H'=1.38$), gives even more information about the structure and composition of a particular plant community.

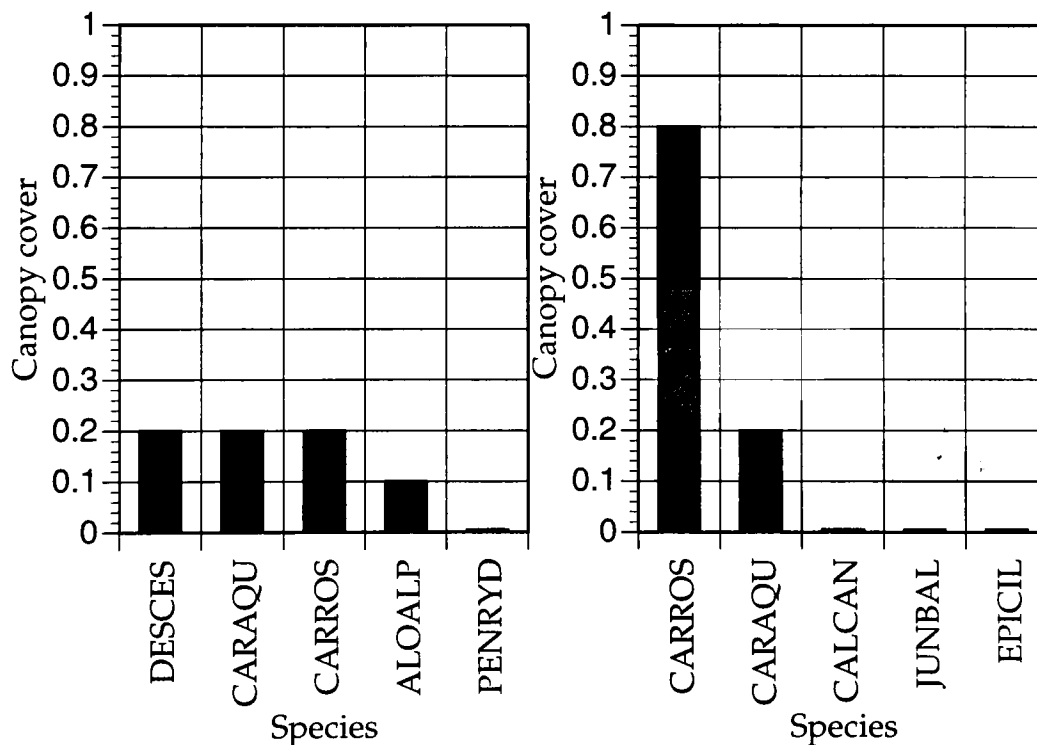


Figure 4. Two sampled plots of the *Carex aquatilis* (water sedge) phase of the *Carex rostrata* (beaked sedge) habitat type with five species each. The community on the left (an early seral community) has a more even species abundance distribution, while the community on the right (a late seral community) has an uneven species abundance distribution

The relationship between Shannon's index or Simpson's index and species richness (Fig. 3) should caution managers against using either of the two diversity indices by themselves as a measure of diversity, especially when comparing different particular plant communities. Note that it is possible to have the same Shannon's H' value for different levels of species richness (trace a vertical line from any value of Shannon's index in Fig. 3). Because of this, that same value could represent both a very even community with few species and an uneven community with a greater number of species.

Correlations

As plant communities become increasingly complex in terms of vertical layers, the correlation between species richness and both Shannon's and Simpson's diversity indices decreases. Grass- and forb-dominated communities typically have fewer species, while tree-dominated communities have more species. Tree-dominated communities are more complex not only because they have more species, but because they have more vertical layers. Species in the upper layers can influence species in the lower layers by casting shade, creating more possibilities for different types of relationships among species (i.e. shading out or providing shade). As mentioned before, diversity indices reflect both richness and evenness. If the correlation between Simpson's index and species richness decreases, Simpson's index potentially signals more information. For example (Table 1), Spearman's rank correlation coefficient is less in more complex communities dominated by shrubs and trees. This suggests that Shannon's and Simpson's index, combined with species richness, may provide more information in tree and shrub communities than in simpler communities dominated by herbaceous species. Fig. 3 supports this, since the range of possible diversity

index values increases as the number of species increases for both Shannon's and Simpson's index.

The correlation between species richness and Simpson's index is less than the correlation between species richness and Shannon's index (Table 1). Put another way, Simpson's index is more independent of species richness, so Simpson's index may offer more information than Shannon's index when used in conjunction with species richness. This advantage needs to be weighed against these indices' other intrinsic properties. For example, Shannon's stronger response to rarer species and Simpson's stronger response to dominant species may be more important features at certain scales. Either diversity index should be used as one of a set of tools that should include species richness, photographs, relative abundance graphs, and *Classification of Montana's Riparian and Wetland Sites* (Hansen and others 1995).

Table 1. Spearman's rank correlation coefficients between two diversity indices and species richness by lifeforms

Diversity Index	Herbaceous types (n=882)	Shrubs (n=1,005)	Trees (n=809)
Shannon's index	0.876	0.799	0.653
Simpson's index	0.812	0.656	0.426

Comparison of Successional Stage to Explain Variation in Diversity Index Values

Given the results of the above correlations, I decided to test whether species richness, Shannon's index, and Simpson's index values would help distinguish between different seral stages within lifeforms. I used the Kruskal-Wallis one-way analysis of variance (Noether 1991), and the rejection threshold for all tests was $\alpha = 0.05$. First, I held species richness fixed within lifeforms, and then I ran the tests for all plots (and therefore all values of species richness) within various lifeforms. At this point, my purpose was to investigate the nature of the indices, rather than to use the indices to quantify diversity between seral stages. That is why I discuss how seral stages can *explain variation in indices*, rather than immediately using the statistical results that follow to make absolute statements about diversity differences between seral stages.

In my first analysis, I tested the ability of early/mid seral and late seral/climax willow plots containing 15 species to explain the variation in Shannon's index. The result was not significant, indicating that seral stage did not explain the variation when holding species richness fixed. Next, I tested the ability of early/mid seral and late seral/climax sedge plots containing five species to explain the variation in Shannon's index. This result was not significant, indicating that seral stages are unable to explain the variation. I repeated this test for different species richness levels with different lifeforms and found similar results. This suggests that although there is a range of both Shannon's index and Simpson's index for a given species richness, categorizing a particular life form by seral stage does not explain this variation.

Table 2 summarizes the ability of seral stage (early/mid seral or late seral/climax) to explain variation in diversity indices by life form, regardless of species richness. Asterisks indicate a significant result using the Kruskal-Wallis test at $\alpha = 0.05$, and indicate that seral stage does explain variation in diversity indices.

Deciduous tree types' seral stages do not appear to explain variation in the value of the Shannon's index or Simpson's index. In non-willow shrub habitat types, seral stage explains variation in both species richness and Shannon's index. This may be the case because Shannon's index is influenced most heavily by changes in rare species which are given equal weight by species richness. Seral stage explains variation in all three diversity measures associated with willow habitat types. From these results, it is not clear whether this is driven mainly by species richness, by evenness, or by a combination of the two.

Table 2. Asterisks indicate significant differences when comparing early/mid seral vs. late seral/climax plots using three diversity measures for six lifeforms

Lifeform (# of plots)	Shannon's Index	Simpson's index	Species Richness
Conifer (194)	*	*	
Deciduous tree (139)			
Non-sedge herbaceous (416)	*	*	*
Non-willow shrubs (164)	*		*
Sedge (352)	*	*	*
Willows (273)	*	*	*

In both sedge and non-sedge graminoid habitat types, seral stage explains variation in all of the indices. Species richness varies dramatically in these types, possibly driving the other indices more heavily than changes in evenness drives them. These communities are structurally simpler than shrub or tree-dominated communities, so perhaps added variation caused by structural layers is being eliminated, essentially cutting out some noise that this simple analysis cannot sort through otherwise. By holding species richness fixed in sedge communities, Shannon's index and Simpson's index could not differentiate between seral stages. This further indicates that species richness might best predict seral stages in graminoid communities at this coarse resolution.

Here, I am viewing succession as two snapshots, rather than as a continuum, in order to seek large scale patterns. This suggests a few possible hypotheses. First, in coniferous ecological types, seral stage does not explain variation in species richness. However, seral stage does explain variation in Simpson's index, which is most heavily influenced by dominant species. This suggests that coniferous habitat types change more in evenness than they change in richness throughout succession. A possible explanation might be that coniferous habitat types start out with a more evenly abundant mix of species (thick stands of mixed shrubs with young conifers scattered throughout), and later tall conifers with dense foliage dominate the site. Increasing shade from maturing conifers does not seem to reduce the number of species, but must either decrease original species' abundance or allow a whole new set of species to become established. Relative abundance graphs (Fig. 5) illustrate the difference between two plots classified within the *Abies lasiocarpa* (subalpine fir) series. In the top graph, *Abies lasiocarpa* (subalpine fir) and *Picea* spp. (spruce)—denoted as ABILAS and PICEAX

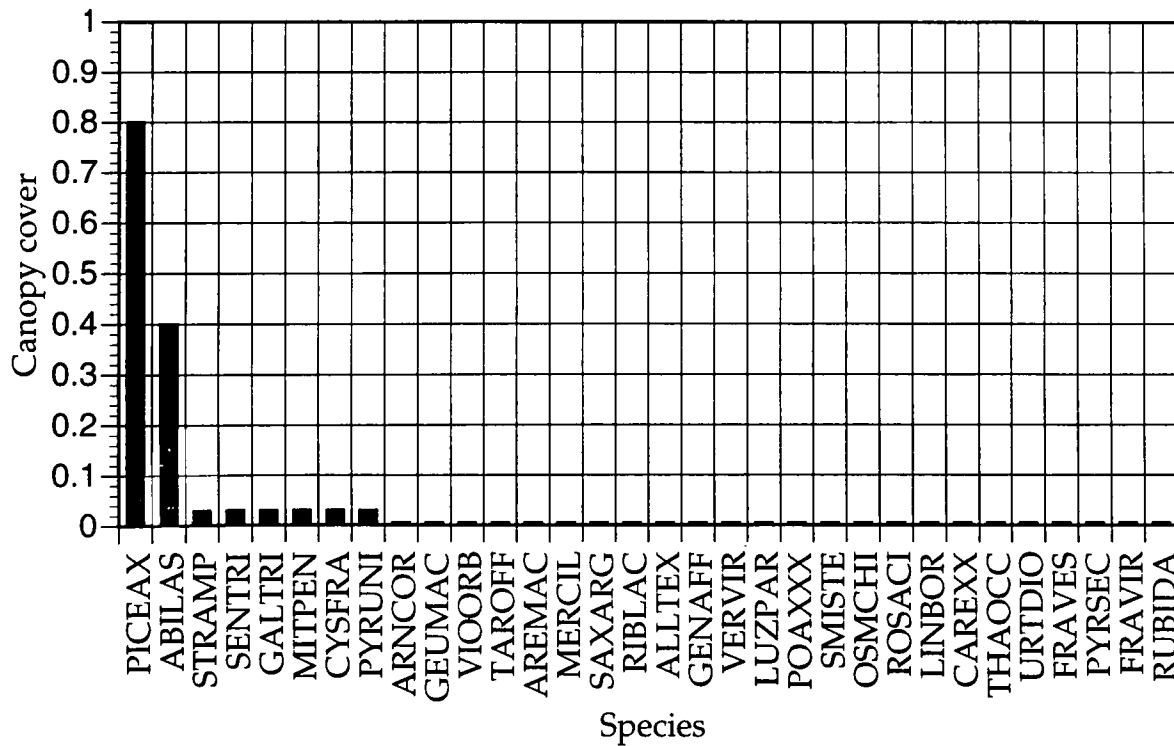
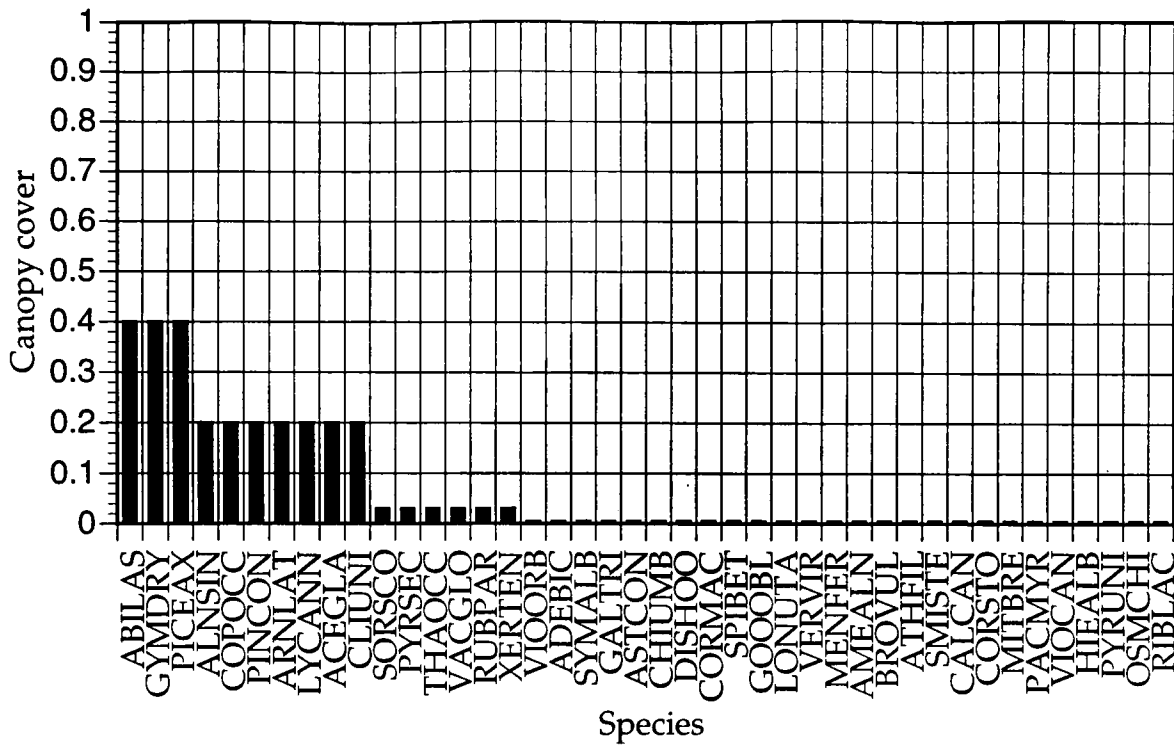


Figure 5. Relative abundance graphs for early/mid seral (top) and late seral/ climax (bottom) coniferous communities

respectively—each cover 40% of the area. *Pinus contorta* (lodgepole pine), *Alnus sinuata* (Sitka alder), *Acer glabrum* (Rocky Mountain maple)—denoted as PINCON, ALNSIN, and ACEGLA—along with a handful of other species each cover 20% of the area. Since these percentages add up to more than 100%, different species obviously occupy the same space because of multiple vertical layers, suggesting that vegetation is very dense on this site. In the lower graph, *Abies lasiocarpa* (subalpine fir) and *Picea* spp. (spruce) clearly dominate the site. The next most abundant species are all forbs, and any shrubs are present in only trace amounts. While the plots in these relative abundance graphs are not at the same location, and therefore do not represent a true successional sequence that actually happened, they do represent the same habitat type, or potential natural community (*Abies lasiocarpa* / *Streptopus amplexifolius* [subalpine fir / clasping-leaved twisted-stalk] habitat type). A habitat type's potential natural community can vary according to the range of abiotic conditions on the site, and can also be somewhat determined by which seeds are present when conditions for germination are right. In this sense, a habitat type creates a set of boundaries that determines a possible superset of species that can make up a plant community. Habitat types also bound possible variation in species composition and abundance over time. A particular plant community on the ground is a special case of the range of possibilities within a habitat type.

Since diversity combines richness and evenness, successfully describing diversity in a vascular plant community to people who have never seen that community can be challenging. These relative abundance graphs help describe species richness by displaying all species' names along the x-axis. Obviously, interpreting that information requires some knowledge of the species present.

Land managers will probably be familiar with many species that occur in their area. Since each species' abundance is plotted on the y-axis, comparing these abundance bars creates a picture of evenness. If all bars are close to the same height, the plant community will have a higher evenness component of diversity. If the bars on the left are dramatically higher, then the plant community is less even, and the evenness component of diversity will be lower. For example, in Figure 3 the early/mid seral plot has 42 species, Shannon's index = 2.67, and Simpson's index = 0.91. The late seral/climax plot has 32 species, Shannon's index = 1.61, and Simpson's index = 0.64. Comparing the two, a 24% reduction in species richness going from the early/mid seral plot to the late seral/climax plot corresponds to a 40% reduction in Shannon's index and a 30% reduction in Simpson's index. Since the two indices that take into account evenness decreased proportionally more than did the number of species, these numbers reflect a decrease in evenness from early/mid seral to late seral/climax.

From this exercise, it is clear that extracting ecological meaning from habitat types' diversity index rankings requires that we understand which component of diversity is driving the rankings. As mentioned above, diversity indices reflect changes in richness and evenness. So while Shannon's index, Simpson's index, and other indices like them came about because people sought a single measure for diversity, the fact that indices lump together two aspects of plant communities' structure can make them very difficult to interpret. By using several indices together, it is sometimes possible to sort out which component (richness or evenness) is driving their values, but if several indices are required to interpret patterns, it may be impractical and perhaps inaccurate to base strong statements about plant community structures on these indices alone.

Lifeform as an Explanation of Variation in Diversity Indices

Strictly speaking, the Komogorov-Smirnov two-sample test is a way to test the ability of a grouping variable (for example, lifeform) to explain variation in a quantitative variable (for example, a diversity index) by evaluating the probability that the two groupings of the quantitative variable come from the same population.

I grouped all 2,702 plots by the six life form categories used to organize ecological types in *Classification and Management of Montana's Riparian and Wetland Sites* (Hansen and others 1995). These categories are conifers, deciduous trees, willows, non-willow shrubs, sedges, and other herbaceous plants. Using the Komogorov-Smirnov two-sample test with a rejection rule of $\alpha = 0.05$, I compared these six groups to each other to see if their diversities came from the same population. Using species richness, all lifeforms were significantly different from each other, except for all combinations of deciduous trees, willows and non-willow shrubs. Using Shannon's index or Simpson's index, all combinations of lifeforms were significantly different from each other with no exceptions. Table 3 provides average values for the three indices by these six lifeforms.

I regrouped the plots into three larger categories: trees; shrubs; and herbaceous species. Using the Komogorov-Smirnov two-sample test again, all three indices distinguished between all combinations of these groupings.

Table 3. Average values of indices by life form

Life form	Species Richness	Simpson	Shannon
Conifer	27	0.80	2.09
Deciduous	15	0.76	1.82
Willow	17	0.74	1.79
Non-willow shrub	15	0.71	1.68
Non-sedge herbaceous	6	0.37	0.47
Sedge	8	0.45	0.95

Comparisons based on species richness are easy to interpret. For example, we can say that on average in Montana, coniferous tree-dominated types have more species present than deciduous tree-dominated types. Interpreting comparisons based on Shannon's index alone would be more difficult, however. For example, we can only say that coniferous tree-dominated types have more of *a combination of species present and a more even distribution of those species present* than deciduous tree-dominated types. Since both species richness and Shannon's index differentiate between coniferous and deciduous types, there remains some question about whether evenness drives the differences in Shannon's index. Viewing this graphically could illustrate the relationship; indeed, Figure 6 suggests that species richness differences drive Shannon's index.

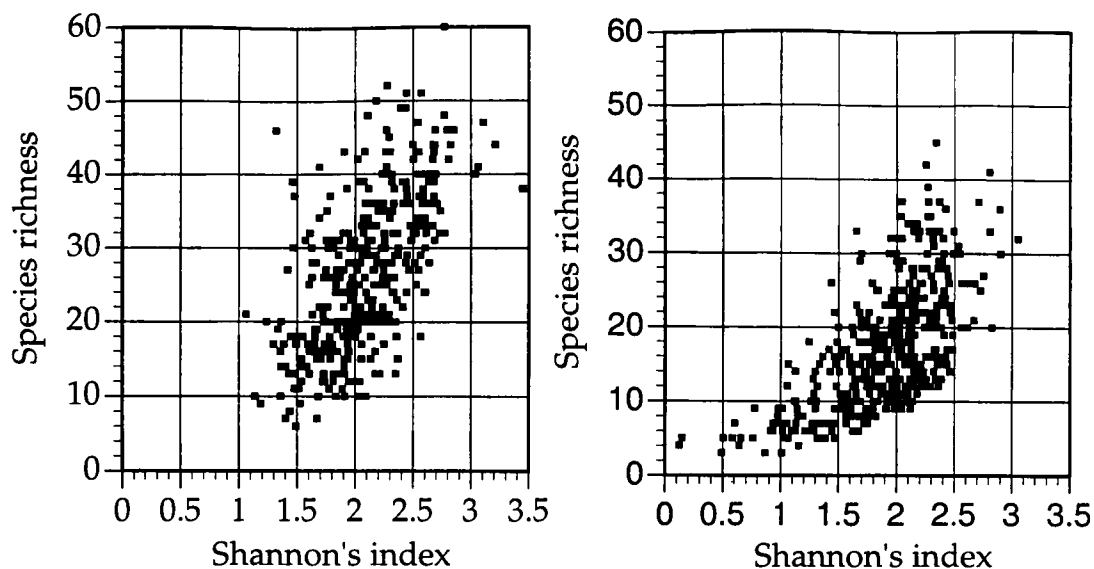


Figure 6. Species richness plotted against Shannon's index for ecological types dominated by coniferous(left) and deciduous (right) trees

Species richness fails to distinguish between willows and other shrubs, while Shannon's index does distinguish between them. This might suggest that willow-dominated types and other shrub-dominated types have generally the same number of species, but species in willow-dominated communities are more evenly distributed in terms of their relative abundance. The graphical comparison (Fig. 7) does not support this, however. There is no clear separation between the two lifeforms' distributions. Willow-dominated types and other shrub-dominated types share the same vertical layers and may be expected to have similar community structures. Therefore comparing willow-dominated types and other shrub-dominated types may not be meaningful. The distinction between willows and non-willows is more qualitative, depending on the unique physiologies and interactions among species within a particular ecological type.

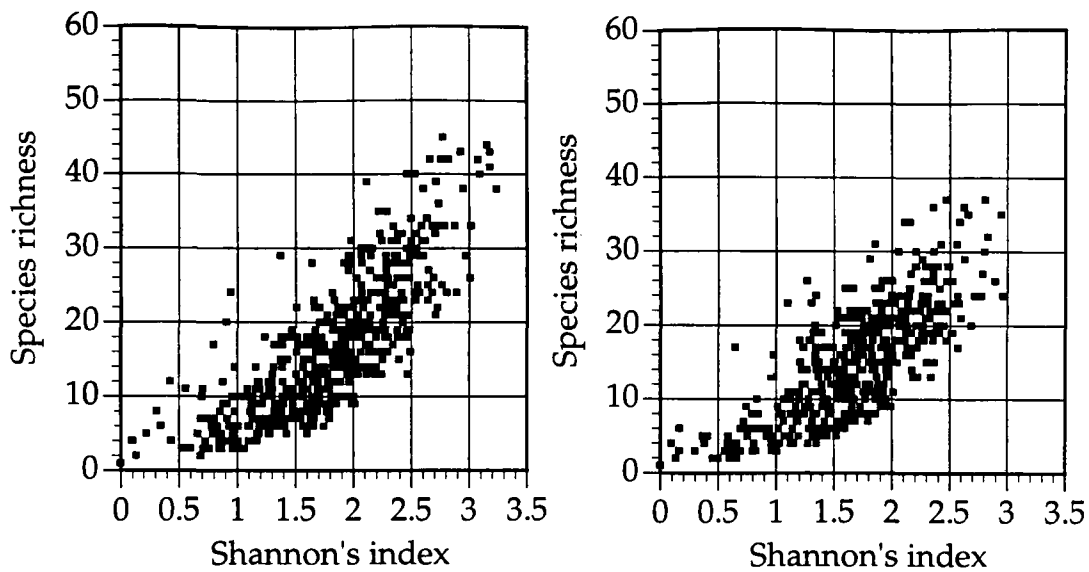


Figure 7. Species richness plotted against Shannon's index for ecological types dominated by willows (left) and by other shrubs (right)

Comparing sedge types with other herbaceous types results in similar problems. In this case, species richness explains the difference between the two groupings, but Shannon's index does not. Viewing the graphical relationship between the two indices and groupings does not reveal any trends (Fig. 8).

Finally, comparing coniferous types with sedge types using both species richness and Shannon's index demonstrates a bivariate graph's usefulness in a more extreme comparison (Fig. 9). Thinking of the Shannon' index/ species richness relationship as a kind of density curve, the simpler sedge types reside in the lower left part of the curve, while the more complex coniferous types reside in the upper right part of the curve.

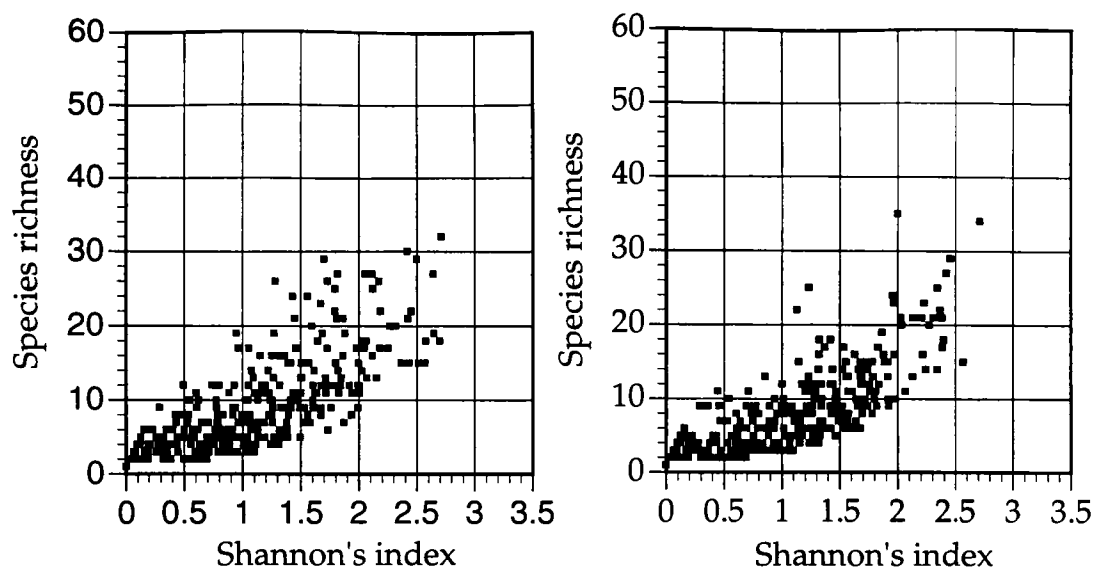


Figure 8. Species richness plotted against Shannon's index for ecological types dominated by sedges (left) and by other herbaceous ecological types (right)

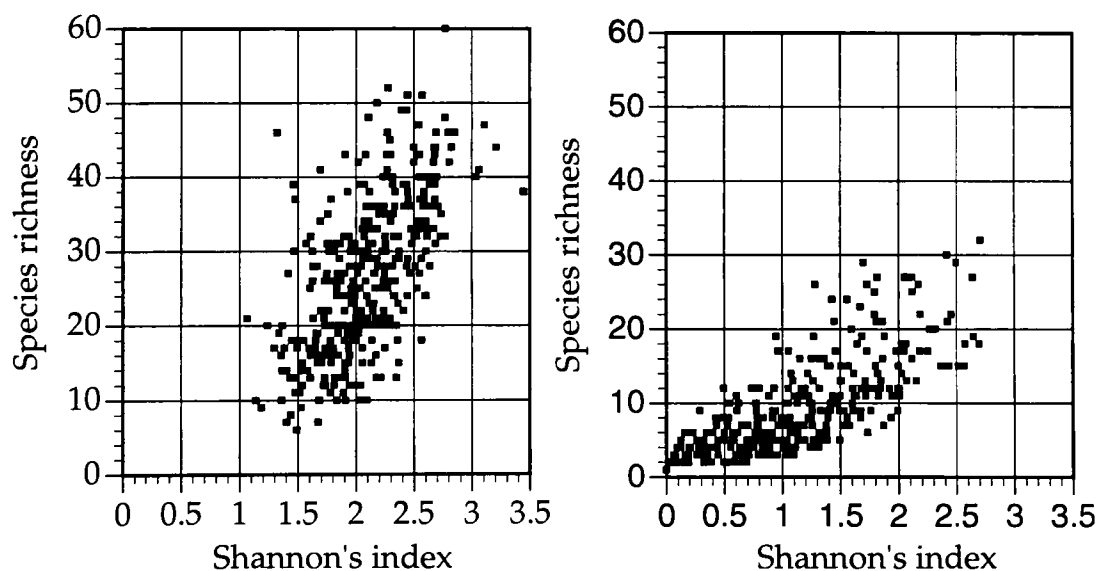


Figure 9. Species richness plotted against Shannon's index for ecological types dominated by conifers (left) and by sedges (right)

Table 4 lists all of Montana's riparian and wetland habitat and community types by average species richness, average Shannon's index, and average Simpson's

index, and further breaks these average values by seral stage. Lewis and others (1988) touted these indices as wonderful tools because they are "...indifferent to species' names while being only concerned with the length of species lists and equitability of proportional abundance. These characteristics make them especially useful as measures of diversity in meeting requirements of the National Forest Management Act." While managing land to maximize diversity indices may meet the requirements of certain laws, this maximizing may not make sense for every ecological type.

For example, the *Carex rostrata* (beaked sedge) phase of the *Carex rostrata* (beaked sedge) habitat type, when split by seral stage, reveals different average values for species richness and the diversity indices. Later seral plots' average three species, while earlier seral plots average nine species. Both Shannon's index and Simpson's index are higher in earlier seral plots. As a sedge community develops, a dense network of rhizomes forms, forcing out other species that colonized the site when the ground was relatively bare, and in the process lowering diversity index values. This rhizomatous network holds streambank soil together, and acts as a sponge to hold water late into the growing season. Sedge communities offer a strong exception to any assumptions that high diversity, as measured by species richness, Shannon's index and Simpson's index, is more desirable than low diversity.

Willow dominated communities display a similar trend. In almost every willow dominated ecological type, species richness, Shannon's index and Simpson's index are lower in later seral plots. Both Shannon's index and Simpson's index decrease as one or more species dominates a site.

In riparian areas, disturbance that produces bare soil and resulting primary succession is a more significant process than it is in uplands. As streams and rivers move across their flood plains, which is a normal process (Leopold 1994), they deposit silt on point bars, creating new habitat for plant communities. Because of this, it is normal for there to be early seral plant communities forming on the new ground. Analyzing the MRWA data set has demonstrated that later seral plant communities often have lower diversities as measured by three different indices. This does not mean that managers should now manage for low diversity, or that the National Forest Management Act should be amended to require low diversity in riparian areas. It simply means that it is natural for there to be a variety of seral stages within the same ecological type occupying the same stream reach. A variety of seral stages, if quantified using the methods in this study, will yield a range of diversity index values.

The indices should not be used alone to characterize diversity, since they require a specific context before anyone can interpret their results. Nonetheless, people will probably continue to use the indices, perhaps only because they are called “diversity indices.” A better name might be “identity-independent assemblage relative distribution indices”—perhaps such a name would discourage misuse. This study provides a tool to understand the indices in the context of Montana’s wetland vascular plant communities, and is not a set of instructions for how to use diversity indices by themselves to quantify management objectives or set up monitoring programs

The indices do help us answer broad questions about diversity in the larger context of Montana’s wetland vascular plant communities, however. Coniferous

ecological types contain more species than deciduous ecological types, and in general later seral plant communities tend to be less evenly structured in terms of species relative abundance than earlier seral communities. Although the MRWA data set does not contain information that quantifies relative wetness, we can develop a hypothesis that wetter ecological types are inherently less diverse than dryer ecological types, and encourage future research in that direction.

Table 4. Average diversity values by ecological types and by seral or disturbance stages. Ecological types are represented with six-letter codes which are the first three letters of the genus followed by the first three letters of the species.

Ecological type Stage	Average by type and seral/disturbance stage			Average by type		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
Coniferous Types						
ABIGRA/ATHFIL				33	2.40	0.85
Early/mid seral	34	2.38	0.83			
Late seral/climax	32	2.43	0.87			
ABILAS/ACTRUB				37	2.34	0.85
Early/mid seral	37	2.54	0.88			
Late seral/climax	38	2.26	0.84			
ABILAS/CALCAN-CALCAN PHASE				30	2.14	0.82
Early/mid seral	28	2.15	0.83			
Late seral/climax	32	2.13	0.82			
ABILAS/CALCAN-LIGCAN PHASE				25	2.07	0.81
All stands	25	2.07	0.81			
ABILAS/CALCAN-VACCES PHASE				30	2.02	0.80
All stands	30	2.02	0.80			
ABILAS/GALTRI				41	2.29	0.83
Early/mid seral	41	2.40	0.86			
Late seral/climax	41	2.17	0.80			
ABILAS/LEDGLA-CALCAN PHASE				27	2.33	0.85
Early/mid seral	32	2.67	0.89			
Late seral/climax	24	2.13	0.83			
ABILAS/LEDGLA-LEDGLA PHASE				23	2.07	0.83
Early/mid seral	17	1.84	0.79			
Late seral/climax	26	2.21	0.85			
ABILAS/OPLHOR						
All stands				34	2.51	0.89
ABILAS/STRAMP-MENFER PHASE						
All stands				19	1.96	0.81
ABILAS/STRAMP-STRAMP PHASE				34	2.28	0.83
Early/mid seral	34	2.33	0.84			
Late seral/climax	33	2.22	0.82			
JUNSCO/CORSTO				17	2.03	0.81
Early/mid seral	17	2.06	0.81			
Late seral/climax	16	1.82	0.76			
PICEA/CALCAN				19	1.78	0.74
Disturbed stands	19	1.74	0.72			
Undisturbed stands	18	1.81	0.76			
PICEA/CORSTO						
All stands				33	2.29	0.82

Table 4 (cont.)

Ecological type Stage	<u>Average by seral/disturbance stage</u>			<u>Average by type</u>		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
PICEA/EQUARV				25	1.70	0.72
Early/mid seral	28	1.85	0.76			
Late seral/climax	23	1.58	0.69			
PICEA/GALTRI				37	2.01	0.73
Early/mid seral	36	2.23	0.83			
Late seral/climax	37	1.76	0.62			
PICEA/LYSAME						
All stands				25	1.81	0.70
PINPON/CORSTO						
All stands				18	1.96	0.81
PINPON/PRUVIR						
All stands				27	2.02	0.81
PSEMEN/CORSTO						
All stands				22	2.06	0.81
THUPLI/ATHFIL-ATHFIL PHASE				24	2.02	0.78
Early/mid seral	27	2.38	0.87			
Late seral/climax	22	1.81	0.73			
THUPLI/GYMDRY						
All stands				27	1.98	0.75
THUPLI/OPLHOR				29	2.26	0.84
Early/mid seral	34	2.43	0.86			
Late seral/climax	25	2.14	0.83			
TSUHET/GYMDRY				25	1.97	0.78
Early/mid seral	25	2.05	0.80			
Late seral/climax	25	1.90	0.76			
Deciduous Types						
ACENEG/PRUVIR				11	1.75	0.75
Early/mid seral	10	1.67	0.73			
Late seral/climax	18	2.37	0.88			
ELAANG						
All stands				12	2.00	0.83
FRAPEN/PRUVIR				15	1.95	0.80
Early/mid seral	12	1.76	0.75			
Late seral/climax	16	1.96	0.81			
POPANG/CORSTO				15	2.01	0.82
Disturbed stands	15	2.01	0.82			
Undisturbed stands	14	2.00	0.82			
POPANG/HERB						
Disturbed stands	13	1.51	0.67			
POPANG/RAB						
Undisturbed stands	12	1.49	0.66			

Table 4 (cont.)

Ecological type Stage	<u>Average by seral/disturbance stage</u>			<u>Average by type</u>		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
POPANG/SYMOCC						
Disturbed stands				13	1.86	0.80
POPDEL/CORSTO				13	1.73	0.76
Disturbed stands	14	1.79	0.77			
Undisturbed stands	9	1.57	0.72			
POPDEL/HERB				12	1.65	0.73
Disturbed stands	11	1.66	0.74			
Undisturbed stands	16	1.62	0.71			
POPDEL/RAB				11	1.45	0.66
Disturbed stands	10	1.31	0.65			
Undisturbed stands	11	1.49	0.67			
POPDEL/SYMOCC						
Disturbed stands				13	1.81	0.78
POPTRE/BERREP						
All stands				27	2.08	0.82
POPTRE/CALCAN				22	2.25	0.84
Early/mid seral	22	2.36	0.86			
Late seral/climax	23	2.15	0.81			
POPTRE/CORSTO				24	2.17	0.83
Early/mid seral	24	2.19	0.83			
Late seral/climax	23	2.06	0.81			
POPTRE/OSMOCC				28	2.04	0.79
Early/mid seral	28	1.99	0.78			
Late seral/climax	27	2.13	0.81			
POPTRE/POAPRA						
Disturbed stands				21	1.88	0.77
POPTRI/CORSTO				18	2.05	0.82
Disturbed stands	18	2.09	0.83			
Undisturbed stands	17	1.87	0.78			
POPTRI/HERB						
Disturbed stands				16	1.60	0.67
POPTRI/RAB				15	1.64	0.68
Disturbed stands	17	1.98	0.80			
Undisturbed stands	13	1.27	0.55			
POPTRI/SYMOCC						
Disturbed stands				19	1.91	0.77
SALAMY				13	1.85	0.79
Disturbed stands	13	1.84	0.79			
Undisturbed stands	13	1.94	0.82			

Table 4 (cont.)

Ecological type Stage	<u>Average by seral/disturbance stage</u>			<u>Average by type</u>		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
Willow Types						
SALBEB						
Disturbed stands				21	2.03	0.78
SALCAN/CARROS						
Early/mid seral	21	2.14	0.82			
Late seral/climax	13	1.46	0.65			
SALDRU						
All stands				17	1.04	0.41
SALDRU/CALCAN						
Early/mid seral	20	1.93	0.77			
Late seral/climax	18	1.63	0.70			
SALDRU/CARROS						
Early/mid seral	21	2.09	0.79			
Late seral/climax	12	1.40	0.65			
SALEXI						
Disturbed stands	11	1.55	0.70			
Undisturbed stands	8	0.94	0.47			
SALGEY						
Disturbed stands				22	2.06	0.80
SALGEY/CALCAN						
Early/mid seral	21	2.15	0.82			
Late seral/climax	12	1.43	0.65			
SALGEY/CARROS						
Early/mid seral	19	2.05	0.81			
Late seral/climax	11	1.55	0.70			
SALLAS						
Disturbed stands	11	1.46	0.64			
Undisturbed stands	7	0.89	0.39			
SALLUT						
Disturbed stands				16	1.66	0.66
SALLUT/CALCAN						
All stands				20	1.90	0.76
SALLUT/CARROS						
Early/mid seral	18	2.07	0.83			
Late seral/climax	8	1.02	0.54			
SALPLA/CARAQU						
Early/mid seral	20	1.92	0.76			
Late seral/climax	12	1.51	0.68			
SALWOL/CARAQU						
Early/mid seral	16	1.85	0.77			
Late seral/climax	8	1.35	0.64			

Table 4 (cont.)

Ecological type Stage	<u>Average by seral/disturbance stage</u>			<u>Average by type</u>		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
SALWOL/DESCES						
All stands				20	1.88	0.77
Non-willow Shrub Types						
ALNINC						
Disturbed stands	20	1.74	0.73	20	1.72	0.72
Undisturbed stands	19	1.59	0.66			
ALNSIN						
Disturbed stands	25	2.36	0.83	20	1.88	0.74
Undisturbed stands	17	1.64	0.69			
ARTCAN/AGRSMI						
Early/mid seral	11	1.58	0.72	11	1.50	0.70
Late seral/climax	8	0.92	0.51			
ARTCAN/FESIDA						
All stands				20	1.85	0.75
BETGLA/CARROS						
Early/mid seral	24	2.21	0.83	22	2.12	0.81
Late seral/climax	14	1.60	0.68			
BETOCC						
Disturbed stands				15	1.72	0.74
CORSTO						
Disturbed stands	15	1.78	0.73	14	1.61	0.67
Undisturbed stands	10	0.90	0.43			
CRASUC						
Disturbed stands				14	1.73	0.73
KALMIC/CARSCO						
Early/mid seral	12	1.54	0.67	14	1.91	0.78
Late seral/climax	15	2.10	0.84			
POTFRU/DESCES						
Early/mid seral	20	1.95	0.77	20	1.92	0.77
Late seral/climax	13	1.66	0.73			
PRUVIR						
Disturbed stands				14	1.66	0.70
ROSWOO						
Disturbed stands				14	1.70	0.73
SARVER/AGRSMI						
All stands				7	1.41	0.70
SHEARG						
Disturbed stands				15	1.95	0.81
SPIDOU						
Disturbed stands	13	1.46	0.65	5	0.75	0.38
Undisturbed stands	4	0.59	0.32			

Table 4 (cont.)

Ecological type Stage	<u>Average by seral/disturbance stage</u>			<u>Average by type</u>		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
SYMOCC						
Disturbed stands				10	1.25	0.57
TAMCHI						
Disturbed stands				10	1.45	0.68
Sedge Types						
CARAQU-CARAQU PHASE				6	0.71	0.35
Early/mid seral	10	1.14	0.53			
Late seral/climax	4	0.45	0.24			
CARAQU-DESCES PHASE				11	1.37	0.64
Early/mid seral	11	1.47	0.67			
Late seral/climax	10	0.99	0.51			
CARLAS				8	1.20	0.59
Early/mid seral	10	1.45	0.69			
Late seral/climax	6	0.88	0.46			
CARLIM				6	1.06	0.55
Early/mid seral	9	1.38	0.70			
Late seral/climax	4	0.70	0.37			
CARNEB						
Disturbed stands				5	0.56	0.27
CARROS-CARAQU PHASE				9	1.21	0.60
Early/mid seral	14	1.41	0.63			
Late seral/climax	7	1.08	0.58			
CARROS-CARROS PHASE				5	0.50	0.25
Early/mid seral	9	0.96	0.45			
Late seral/climax	3	0.38	0.20			
CARROS-DESCES PHASE						
All stands				11	1.50	0.67
CARSOO				16	1.98	0.78
Early/mid seral	21	1.85	0.70			
Late seral/climax	13	2.04	0.81			
CARSIM				13	1.25	0.54
Early/mid seral	17	1.64	0.68			
Late seral/climax	8	0.77	0.37			
Herbaceous Types (except for sedges)						
AGRSMI				10	1.15	0.52
Early/mid seral	12	1.38	0.61			
Late seral/climax	4	0.48	0.25			
AGRSTO						
All stands				21	2.39	0.88

Table 4 (cont.)

Ecological type Stage	<u>Average by seral/disturbance stage</u>			<u>Average by type</u>		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
BROINE						
All stands				4	0.71	0.42
CALCAN				12	1.38	0.60
Early/mid seral	14	1.80	0.76			
Late seral/climax	9	1.01	0.46			
DESCES				14	1.71	0.73
Early/mid seral	15	1.79	0.75			
Late seral/climax	10	1.47	0.67			
DISSPI				4	0.76	0.41
Early/mid seral	5	0.96	0.52			
Late seral/climax	3	0.50	0.27			
ELEPAL				6	0.82	0.41
Early/mid seral	7	1.00	0.50			
Late seral/climax	2	0.13	0.06			
ELEPAU				9	0.99	0.46
Early/mid seral	11	1.31	0.58			
Late seral/climax	6	0.73	0.36			
EQUFLU				3	0.31	0.17
Early/mid seral	3	0.49	0.27			
Late seral/climax	1	0.01	0.00			
GLYBOR				4	0.84	0.47
Early/mid seral	4	0.98	0.51			
Late seral/climax	3	0.73	0.43			
GLYLEP				6	1.06	0.59
All stands						
HORJUB				9	0.46	0.17
All stands						
JUNBAL				6	0.98	0.46
Disturbed stands						
PHAARU				5	0.51	0.24
Early/mid seral	8	0.96	0.46			
Late seral/climax	3	0.18	0.08			
PHRAUS				2	0.45	0.26
Early/mid seral	3	0.75	0.44			
Late seral/climax	1	0.00	0.00			
POAPAL				6	0.88	0.41
Disturbed stands						
POAPRA				12	1.48	0.67
Disturbed stands						
POLAMP				2	0.15	0.08
Disturbed stands	3	0.38	0.20			
Undisturbed stands	1	0.00	0.00			

Table 4 (cont.)

Ecological type Stage	<u>Average by seral/disturbance stage</u>			<u>Average by type</u>		
	Richness	Shannon	Simpson	Richness	Shannon	Simpson
SALRUB						
All stands				3	0.32	0.16
SCIACU				4	0.55	0.30
Early/mid seral	5	0.91	0.49			
Late seral/climax	2	0.27	0.16			
SCIMAR				2	0.30	0.16
Early/mid seral	5	1.32	0.70			
Late seral/climax	2	0.05	0.02			
SCIPUN				5	0.70	0.36
Early/mid seral	6	0.97	0.50			
Late seral/climax	2	0.06	0.02			
SENTRI						
Disturbed stands				17	1.84	0.75
SPAPEC				4	0.58	0.31
Early/mid seral	6	0.94	0.48			
Late seral/climax	2	0.18	0.11			
TYPLAT				2	0.27	0.15
Early/mid seral	4	0.66	0.37			
Late seral/climax	1	0.06	0.03			

DISCUSSION

To discuss biodiversity is to discuss all life, which would be impractical in any kind of local land management situation, so any discussion must be bounded. We must choose categories and units of life, geographic locations, and measurement scales. We need to decide whether to operate at the genetic, specific, generic, community, inter-community, landscape or global scales. We must also keep in mind that the public's perception of biodiversity is vague. Providing a context for discussing biodiversity can add some clarity to the issue.

Asking specific questions can help define what "biodiversity" means in a particular context. How does the number and types of vascular plants growing together near streams in Montana affect the way those streams trap sediment, buffer floods, grow forage, hold banks together, provide later summer flows, and create homes for other forms of life. Can these particular arrangements and quantities of plants indicate a riparian area's potential for supporting roads, surviving fires, growing timber, withstanding livestock grazing, or providing stable campground locations?

A standard biodiversity definition that includes the variety of life at different scales and the processes that affect interactions among the different components of this variety only provides a scant framework for understanding biodiversity. "Biodiversity" is a sign for a way of thinking about a question. "Economics" is a similar symbol. When I hear that an argument is to be an economic argument, I prepare for a discussion of material value, since that is where my finite knowledge of the subject forces me to classify it. If a regulation ordered me to

manage for economics, my mind would spin forever in the abstract, and I would fail for not knowing where to begin. Managing for biodiversity is similarly impossible, without a context.

Biodiversity, if it is to be understood, must be broken down. The Council on Environmental Quality (CEQ) breaks biodiversity into components that are easier to grasp (Council on Environmental Quality, 1993). CEQ's general principles for considering biodiversity in environmental management include:

1. Take a "big picture" or ecosystem view.
2. Protect communities and ecosystems.
3. Minimize fragmentation. Promote the natural pattern and connectivity of habitats.
4. Promote native species. Avoid introducing non-native species.
5. Protect rare and ecologically important species.
6. Protect unique or sensitive environments.
7. Maintain or mimic natural ecosystem processes.
8. Maintain or mimic naturally occurring structural diversity.
9. Protect genetic diversity.
10. Restore ecosystems, communities and species.
11. Monitor for biodiversity impacts. Acknowledge uncertainty. Be flexible.

Several scientists present arguments that support or do not support aspects of each item on this overall list. These researchers also propose specific strategies that apply these principles (Noss and Cooperrider 1994; Grumbine 1992). Here, rather than provide a detailed discussion of these arguments and strategies, I

point out that these principles are useful, and help to narrow the subject of biodiversity into concrete goals. Instead of managing for biodiversity, or even worse managing to maximize biodiversity, planners, policy makers and regulation writers should use this list to select elements of biodiversity that can be identified through concrete examples. For example, it makes more sense to set a management goal to maximize connective corridors for large animal migration than it does to set a management goal to maximize biodiversity on a landscape. The former goal is concrete, and leads one to assume that someone has established a reason for providing migration corridors. The latter goal may meet the requirements of a policy directive, but land managers would be left without a basis for designing strategies to meet the goal.

Consider the riparian component of a landscape in Montana. As hydrology, elevation and soil types change, so will the ecological types described in *Classification and Management of Montana's Riparian and Wetland Sites* (Hansen and others 1995), which are useful units for thinking about managing a landscape. There are different ecological types present, and the same types are present at different successional stages. For example, consider a recent alluvial bar, which is a deposit of silt and gravel left behind after a flood passes through. Cottonwood seedlings establish, along with willow seedlings. From a species perspective, the diversity is low at this early succession stage. As the plant community changes through time, the number of species increases as the number of vertical layers increase and changing microclimate conditions (shade, for example) allow species to move in that could not grow on the bare, exposed soil. As this site changes, another alluvial bar will appear somewhere else along the stream, so that a whole range of successional stages (and a range of species richness) exist at

the same time within the same landscape, in the same ecological type. Sedges establish along a low-gradient section of the same stream. As this species' rhizomes dominate the soil sub-surface, other plants are excluded, choked out by the dense, monospecific root network. This sedge meadow, a wetland manager's pride and joy, undergoes a reduction in species richness as it moves toward its potential natural community.

Any policy that encourages management for high diversity without specifying a context will pit land managers against the natural processes they are trying to encourage or complement through their actions. Similarly, managing for mid to late seral stages ignores the dynamic nature of riparian systems, which must undergo primary succession to colonize natural bare soil that will eventually result in potential natural communities. Ecological systems must be young before they can become old. The Rocky Mountain Biological Diversity Assessment (USDA 1992) suggests that riparian areas be managed for mid to late seral successional states. Land managers at all levels must consider that riparian areas in particular are in a state of flux caused by shifting stream channels and continual sediment deposition. Policies must consider: 1) early successional plant communities play a vital role in riparian systems; 2) all successional stages should remain extant within a riparian system; and 3) the portion of a riparian system represented by each successional stage will always be in flux.

In addition to their linearity, riparian systems have width, represented as a flood plain. Depth to the water table varies, creating a range of possible potential natural communities. Since fewer plant species can grow in saturated conditions, ecological types nearest the stream, or where the water table is close to the

surface, have the lowest species richness. This is important for managers to note. Lowering of the water table or dewatering of a stream is often considered to negatively affect the ability of a stream to function (USDI 1993), although this dewatering can occur naturally. As a very wet ecological type dries out, its diversity may increase, particularly in the case of sedge-dominated ecological types.

For example, the *Carex rostrata* (beaked sedge) habitat type has three phases. Ranked from wet to dry, these are the *Carex rostrata* (beaked sedge) phase, the *Carex aquatilis* (water sedge) phase, and the *Deschampsia cespitosa* (tufted hairgrass) phase. Referring to Table 4, average species richness for the *Carex rostrata* (beaked sedge) phase is five, average species richness for the *Carex aquatilis* (water sedge) phase is nine, and average species richness for the *Deschampsia cespitosa* (tufted hairgrass) phase is eleven. Both Shannon's index and Simpson's index increase in the same manner. At some point, lowering the water table combined with grazing disturbance could cause any phase of the *Carex rostrata* (beaked sedge) habitat type to shift to a shallow-rooted herbaceous ecological type like *Poa pratensis* (Kentucky bluegrass), with an average species richness of twelve. Here is a case where an increase in the number of species may be negative, indicating a potential risk to a stream's ability to function. Monospecific ecological types like sedges need water to become established. Once established, however, they act as a sponge, holding water in place. Without water inputs, they can dry up and create spaces for species less tolerant of saturated conditions. This area requires more research.

Lowering the water table can also decrease diversity. For example, when some channels in eastern Montana become incised, the *Agropyron smithii* (western wheatgrass) habitat type will replace the *Artemesia cana/Agropyron smithii* (silver sagebrush/western wheatgrass) habitat type (personal observation). Here, Shannon's index and Simpson's index detect the shift in diversity, decreasing from 1.50 to 1.15, and from 0.70 to 0.52 respectively, while species richness only decreases from eleven to ten. This is probably due to the loss of a vertical layer represented by only one species which accounts for a substantial canopy cover. Shannon's index and Simpson's index are sensitive to changes in canopy cover while species richness is not.

Tracking changes in the number of species and their associated canopy cover in a particular habitat type may be a potent monitoring tool. Vegetation, which is very visible, could be used to detect less visible fluctuations in the quantity of available water beneath the soil surface. Diversity indices could be applied in this type of situation, as long as relationships between plant community diversity and water table depth have been established through a well-designed study.

Shannon's and Simpson's indices can reflect changes in more complex ecological types. For example, as wetland coniferous types approach their potential natural community, their species number remains essential the same as when they were in an early to mid seral stage (Table 4). A count of species will not reflect change, as it might in simpler ecological types. However, as a conifer type approaches its potential natural community, Shannon's index and Simpson's index decline, indicating a less even distribution of species. This makes sense if you picture a fire's aftermath, with sun-loving shrubs and forbs dominating a site, and conifers

beginning to poke up through the deciduous mass of low growth. In this early seral scenario, no one species dominates the site. However, as the conifers grow, they create a closed canopy and they clearly dominate. While the species number remains the same, the composition shifts to smaller species that can subsist on less light. Each species that is not among the dominant conifers accounts for a very small amount of cover, although many of these physically smaller species may be present.

A landscape can have many different ecological types, so another way to think of diversity is in terms of the number of ecological types, their distribution, and the number of seral stages represented within these types (gamma diversity).

Maximizing these still does not make sense, unless there is a specific reason to do so, and a well reasoned context for deciding that more is better.

For example, it is possible to compare the diversity of types and seral stages among different riparian corridors in intermittent tributaries to the Blackfoot River on the East side of the valley between Bonner and Potomac, Montana. A pristine tributary may be monotypic (as opposed to monospecific—note the scale change) over long stretches. A moderately managed tributary may be very diverse in terms of ecological types if it contains patches of uncut timber mixed in with recovering clearcuts of varying ages and resulting seral stages. An entirely clearcut drainage might again be monotypic. A person on Wall Street in Manhattan whose portfolio is dominated by timber stocks would prefer low ecological type or landscape diversity for different reasons than the preservationist, while the wildlife manager might choose the higher diversity

landscape because he believes that more patches, and therefore more edges, make good large game habitat.

Since “pristine” and “clearcut” could be represented by the same landscape diversity number, and they are arguably very different landscapes, some qualitative representation would be necessary to clear things up. One way to quantify landscape diversity would be to substitute ecological types for species in the formulas for species richness, Shannon’s index, and Simpson’s index. For example, a plant community with 20 species has a species richness of 20, and a geographic area that contains 20 ecological types would have an ecological type “richness” of 20. Substitute proportion of total area that each habitat type covers for the species proportion in the Shannon’s index and Simpson’s index formulas.

Seral stages will also be different, and these could be similarly quantified if seral stage is an important part of any management context. Pielou (1975) describes how Shannon’s index in particular can be aggregated across different scales. While her example uses species, genus, and family in biological collections, the mathematics could probably be applied to seral stages and ecological types. From a more qualitative point of view, if logging has increased *Centaurea maculosa* (spotted knapweed), that may negatively effect biodiversity, according to the CEQ principles. Eliminated wildlife corridors, impacted rare species, raised water temperature, lost structural diversity, or rare genotypes turned into plywood may be what truly concern land managers. Applying indices to management at this scale will only be useful if a clear relationship is established between the values of the indices and management goals.

Attempting the earlier comparison between willow and non-willow shrub communities from a more qualitative approach would rephrase the question in terms other than which community has a greater combination of richness and evenness. Rather, managers should think in terms of their management context, and use the CEQ's biodiversity management principles to help phrase meaningful questions. Where a particular ecological type sits on the landscape, and how it relates to its neighboring ecological types can inspire a meaningful question. If a *Symphoricarpos occidentalis* (western snowberry) community type dominates a riparian area across a fence from a *Salix geyeri* /*Carex rostrata* (Geyer's willow /beaked sedge) habitat type, the *Symphoricarpos occidentalis* (western snowberry) community type probably developed because the land on that side of the fence was managed differently from the *Salix geyeri* /*Carex rostrata* (Geyer's willow /beaked sedge) habitat type's side of the fence. *Classification and Management of Montana's Riparian and Wetland Sites* (Hansen and others 1995) describes these ecological types in great detail. The difference in current ecological types may be a result of decisions made 50 to 100 years ago. A manager may decide that the *Salix geyeri* /*Carex rostrata* (Geyer's willow /beaked sedge) habitat type may need more protection than the *Symphoricarpos occidentalis* (western snowberry) community type since the former is more likely to change when it is disturbed. In a fragmented landscape where patches of shrub communities are separated by farmed tracts, the *Salix geyeri* /*Carex rostrata* (Geyer's willow /beaked sedge) habitat type might warrant even more intensive protection efforts due to fewer nearby available seed sources that could replace the type if its current site is disturbed. If the *Symphoricarpos occidentalis* (western snowberry) community type harbors non-native species, this might provide a reason for managers to seek less of it on their lands.

Willows are one indicator of a healthy, functioning riparian system since their dense, woody roots hold streambank soils together (Hansen and others 1995), and for this reason, maintaining willow-dominated ecological types may be a management goal. On the other hand, once a site is dominated by *Symphoricarpos occidentalis* (western snowberry), that site may have lost some of its ability to perform those functions. If either of these ecological types is unique in a landscape, then that type should receive special attention. This approach simply applies the CEQ's synopsis of biodiversity concerns into a simple, reasonable way to evaluate the more abstract concept "biodiversity."

Understanding the biodiversity of a landscape means much more than simply counting species and examining community structure graphs. While this is important for land managers to understand, it is also important to see that diversity indices, species richness, ecological type classifications, photographs, and graphical representations of plant communities are all simply tools. Rather than condemn any one of these tools as useless, we should work hard to understand their limits and to clearly define the context where they will be applied. In riparian areas, a variety of seral stages, and a variety of hydrologic and soil conditions produces a variety of diversities. Diversity indices send different signals based on the ecological types they are used to quantify, and these diversity indices must be used together with species richness for their signals to be understandable. Instead of setting numerical targets for diversity in riparian areas, land managers and policy makers must think in terms of fragmentation, rare and ecologically important species, vertical layers, wildlife habitat and riparian areas' functions. Once these concepts have been translated into objectives, diversity may then be useful as a way to monitor those objectives.

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