

If Biodiversity Is The Answer, What Is The Question?*

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Abstract

The theoretical concepts of species diversity, biodiversity and their relatives were invented in an attempt to capture the complexity of natural ecosystems in a single number. This value represents the number of species present, the number of individuals in each species or similar numbers. Alternate approaches to the single-value index include statistical models of species abundances. With diversity indices calculated with equations taken from information theory, cryptoanalysis and thermodynamics, it is not surprising that these concepts cannot be validly applied to the real world. However, modern computer hardware and software allow for multiple, spatial variables to be examined simultaneously using map algebra for spatial analyses using a GIS (geographic information system). Mathematically rigorous analyses using spatial statistics and fuzzy logic permit us to objectively answer the questions that the diversity concepts tried to answer: why do we find the plants and animals where we do, and why do we observe the variations in distribution patterns?

Introduction

Ever since the concept of diversity was expressed by R.A. Fisher (Fisher et al., 1943), it has been a major area of ecological theory. The meaning of diversity has changed from species richness (Fisher et al. 1943 and Margalef 1958) through a combination of species richness and equitability (Shannon & Weaver 1949; Simpson 1949; and Pielou 1977) to the suggestion by Hurlbert in 1971 that it is a non-concept. In the early 1980s, I conducted post-doctoral research on diversity indices which resulted in a peer-reviewed journal publication (Shepard 1984).

Since that time, I've been focused on practical issues rather than theoretical ones, and I've come to agree with Hurlbert and Pielou (see below) that while diversity is a good concept, it is not of practical value. Therefore, my three goals for this talk are:

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1. To have you understand the underlying reasons for the development of species diversity indices.
2. To have you understand why the whole concept is wrong outside of ecological theory, and why trying to apply it leads to poor management decisions.
3. To have you leave this session feeling positive that there are better methods that actually accomplish what these indices were thought to measure.

As far as I can tell, "biodiversity" is the ecologic term "species diversity" made into a more easily accepted format for general consumption. "Biodiversity", according to one definition I found, includes the concepts of genetic diversity and ecosystem diversity. These latter two terms are either biologically and ecologically meaningless in pragmatic ways, or they cannot be measured. For example, what is the meaning of "genetic diversity"? Shall we try to count all the allelic variation in a population and compare that to some threshold value, or to another population? Or, for "ecosystem diversity", how shall we define the boundaries of each ecosystem? The definition I found of "ecosystem diversity" was the number of different ecosystems found on the earth. Well, counting them, and defending the way you went about counting them, could certainly occupy many years of one's life, but to what value? I suggest that it's a meaningless measure.

Suppose, to follow this thought just a little further, it was possible to calculate some index of ecosystem diversity both before and after the eruption of Mt. St. Helens in southwestern Washington in May, 1980. Or to do the same thing for Yellowstone National Park in 1987 and 1989, before and after the extensive fires of 1988. What could we possibly say about these numbers that would provide any management insight or advance our understanding of the natural world? Perhaps I should have titled this paper, "Sacred Cows Make the Best Hamburger".

When I first entered graduate school in 1972, I quickly became deeply involved in the concept of species diversity. It was a major theme of most of my ecology courses. While I understood the concept at the superficial level, I was bothered by something, but I could not explain what bothered me. It took several years until I understood just what disturbed me. And this is what I will explain to you today. Because the concept was so pervasive in ecology and it continues today in the broader environmental and conservation fields I did a post-doctoral research project on a possible alternative. Why this alternative did not catch on I can explain only by academic politics. Regardless, I have been thinking about the problem ever since because it comes up quite regularly in my work for the mining industry. Today I am convinced that all these indices and species abundance models are too narrow in focus when we consider all the tools at our disposal.

Given all this introduction, it is appropriate to begin by considering the *raison d'être* of species diversity (or biodiversity). It is now time to explain the question for which biodiversity has for too long been proposed as the answer.

We humans can be divided into two categories: those who categorize things and those who do not. In its elemental form, the question for which biodiversity has been proposed as an answer is: **How can we capture the complexity of the natural world in a summary number for evaluation and comparison purposes?** Many good minds set off on the search for an answer, and they borrowed concepts from other disciplines to develop answers. I consider several of these answers today. Not too theoretically or mathematically, but looking at the important aspects and seeing where the assumptions proved false.

Some Approaches to Species Diversity

Some time during the early 1940s the era of the naturalist started being replaced by that of the quantitative ecologist. Not being content to simply put names on plants, animals and other organisms, the latter had to count and differentiate among places, times, groups and other divisions. Ecology, however, is a synthetic science built on many others, so it was natural for ecologists seeking a way of comparing groups of species populations to look to other disciplines for methods and answers.

Here I will ignore the twin morasses of genetic and ecosystem diversity and focus on species diversity because that is really the major component (or, the same thing as) biodiversity. The common definition of species diversity is "the number of different species in a given region". This is also called "species richness", and it looks like a nice measure of something real and meaningful. But, how do we interpret the numbers? Suppose there are 8 species in one area of a given size and 33 species in a similarly-sized area only a few kilometers away? Is one better than the other? What if the first is a site on the Snake River plains in south-central Idaho and the second is a tree-filled draw on one of surrounding mountains?

If species number is not a useful measure, perhaps we can improve on it by adding a relative abundance component. That is, the number of individuals in each species. Now we really have a good metric that has meaning for us and the systems we study. But, wait! Consider this situation: two reclaimed mine sites in Colorado. Both support a bird population of 100 individuals in 10 species. One site has 10 individuals in each of the 10 species. The other site has 91 individual in one species and 1 bird in each of the other 9 species. Which is the more diverse?

When we apply one of the oldest diversity indices, the Shannon (or Shannon-Wiener) index

$$H' = \sum p_i \log p_i$$

we discover that the even distribution has a higher value. This index was originally published in a 1949 cryptographic paper as a measure of the information content of the next data chunk in a coded message. There is no compelling argument that such a measure yields biologically meaningful results when applied to populations of plants or animals. Despite all sorts of mathematical

manipulation, there is still no objective measure of difference between any two values, a threshold value between "good" and "not good" index values, or a way to use this in mined land reclamation or any other practical application.

The Shannon index is a special case of a more general class of functions used in the mathematical theory of information (as applied to cryptographic analyses). The Simpson index uses s kinds of symbols, of which a proportion p_i are of the i^{th} kind, to produce the function

$$H_\alpha = \frac{\log \sum p_i^\alpha}{1 - \alpha}$$

H is known as the entropy of order of the code (equivalently, of the set $\{p_i\}$). And, as α reaches its limit at 1, this Simpson index reduces to the Shannon index.

So, we've moved away from information theory in the context of crypto-analysis to the domain of thermodynamics. Entropy, of course, is a measure of disorder. We ecologists do borrow heavily from other disciplines in our attempts to get metrics for use on the highly complex systems that are the natural world. We tend to forget to see if the underlying assumptions really are applicable to biological populations, or to the dynamics of ecosystems.

As a matter of fact, we either tend to forget what E.C. Pielou wrote, or we are not taught this in our courses: "It cannot be too strongly emphasized that fancied links between the information-theoretic concept of information' and the diversity of an ecological community are merely fancies and nothing more" (Pielou, 1975). This is the first point I want to make. And remember that questioning the value of diversity indices or other measures is neither a new idea nor originated with me; it is at least 30 years old.

We could go on, discussing the measurements of fully-censused communities, large communities, evenness and equitability, hierarchical diversity, and so on. However, I did start by saying that I will not make this too mathematical because I do not want your eyes to glaze over or have you fall asleep and miss the important points.

Even if we considered the more complex metrics, such as the Index of Biotic Integrity, and the Rapid Bioassessment Protocol to characterize aquatic systems we are still missing the point. All of these metrics suffer from an overabundance of theory and mathematics but a shortage of biological or ecological meaning. Let me start discussing some of the shortcomings of these diversity indices with a brief example of how indices can be mis-applied because too few people dug into the underlying assumptions before taking it out of the box and using it.

Problems in Application

The Shannon, Simpson, Brillouin and other diversity indices assume that the numbers used to calculate the index come from statistical samples. That is, that the samples represent the relative proportions of each species in the entire

population. While this may be true in terrestrial systems, it certainly is not true in aquatic systems.

Consider the task of characterizing the vegetative cover on an area that will be used as a reference site for assessing revegetation success during mine reclamation. We will further assume that the site is in the Great Basin and is vegetated by sagebrush, rabbitbrush, bunch grasses and forbs with juniper and ponderosa pine on the hill sides. We have decided, a priori, that our sampling design will be stratified random. Before leaving the office, we look at a topographic map of the area and randomly pick a dozen points and a direction from each point in which we will run our 100 meter sampling transect.

We get to the field and we use a GPS receiver to locate the points we have pre-selected. We lay out the transect sampling line and note the vegetation every 5 meters along the line, and within 1 meter of the line on either side. When we get done, we look at what we have done and we notice that we have managed to avoid including any of the trees in our sampling transects. Oops! What do we do now? The answer we choose is not pertinent to today's discussion of diversity, but it makes the point that we can see the complete population of vegetation from which we take statistically-valid samples.

In aquatic ecosystems, we cannot acquire samples in the statistical sense. What we have are collections of individuals, and we have no idea whether or not our collection represents each species' true relative abundance in the population. Anyone who has used a Surber or Hess net in a first-order mountain stream in the Intermountain West, for example, knows that the large stonefly, *Pteronarcys californica*, can burrow into the substrate faster than we can, and they often escape capture. Similarly, if we use a net with a small mesh size, rapidly-flowing water can back up in the net and flush out invertebrates or algae we are trying to collect. But, if we use a mesh size too large, then the smaller organisms are carried right through it by the water and we get only the larger specimens. Or, if we are sampling in a pit lake or a reservoir with any type of grab sampler (Ponar, Eckman), we have no way of knowing in advance what we might collect because we are dropping the sampler into an area we cannot see.

So, the second important point for you to remember is that any sort of diversity index that assumes the numbers you have are population samples, may be applicable in terrestrial ecosystems, but they are mathematically invalid in aquatic ecosystems where we deal with collections of organisms, not samples.

Whenever a collection is censused or a community sampled, the resultant data consist of a list of the species in the collection or sample together with a statement of the quantity of each species. These quantities may be expressed as numbers of individuals, biomass values, dry weights, cover values or any measure that is appropriate. For convenience we will assume that the quantity of each species is measured by counting individuals, but this does not affect in any way the generality of our discussion.

Another problem with diversity indices is that of mixed taxa collected in the field. This is most prevalent when collecting, identifying and counting invertebrates, but it happens with plants, birds and small mammals, too. The prob-

lem is evident when you look at a so-called "species list" and discover a mix of species, genera, families and orders. How often we see reports of aquatic populations that includes the infamous "miscellaneous dipteran larvae". Sure, many of the true flies need to be reared to adulthood before they can be identified to the species level, but they may account for 90 percent (or more) of the numbers of individuals, biomass, and production in the ecosystem. We certainly do not learn anything useful when mixed taxonomic levels are combined into a single index of diversity.

From data at a consistent taxonomic level diversity indices may be determined or estimated. But a diversity index is merely a single descriptive statistic; one of many needed to characterize the population assemblage and a very difficult one to interpret meaningfully. The belief (or superstition) of some ecologists that a diversity index provides a basis (or talisman) for reaching a full understanding of species population structure is wholly unfounded. A species diversity index is analogous to a statistical sample's variance. I hope that you agree that detailed study of the distribution of a quantitative measure entails more than merely calculating its variance. But, I do not want to push this analogy too far and imply that such indices have more use than they do.

Now that I have explained why diversity indices are not appropriate, it is time to look at alternative measures. Then we will consider how all this fits into the question of characterizing, classifying and comparing biotic components of ecosystems, with emphasis on mined land reclamation.

Classical Alternatives

If diversity indices are analogous to a single statistic, variance in this case, that is part of the description of a distribution of values, we should broaden our search for a useful tool to the distributions themselves. Quite a few population distribution models have been developed and supported. Each model has strengths, weaknesses, and applicability to different ecosystem types or situations. One of the problems we encounter is that ecological theory can come up with very elegant, mathematically sound concepts that prove impossible to implement in the real world. So we will have to be aware of this as we consider potential answers to our question, What can we say about this assemblage of populations that gives us useful, practical insight?

One approach is to apply models of species-abundance distributions. When we are interested in the composition of species populations in a given area, we often find several similar species of apparently similar requirements, but with each of the species greatly differing in their relative abundances. Sometimes the differences can be explained in terms of habitat differences: the abundance of a species may be proportional to the relative amount of space available to it (in terms of suitable habitat). Even when we determine there is a high correlation between a species' abundance and the habitats it needs, we still have not explained why the species have evolved such varying tolerances for habitat that we observe. Distribution models may help ecologists account for the

observed relationships in species abundances.

We can tabulate species abundances in two distinct ways, as *ranked-abundance lists* and as *species-abundance distributions*. The method chosen depends on the number of species in the collection (or sample) that are described by a set of data. If the data contain only a few species it is better to list the number of individuals in each, ranking those numbers from largest to smallest; that is, we compile a *ranked-abundance list*.

However, if the collection is very large and contains numerous species, of which several have exactly one individual, several have exactly two individuals, and so on, the most convenient way of summarizing the data is as an observed frequency distribution, giving the frequency of species represented by 1, 2, 3, and so on individuals. The result is a *species-abundance distribution*.

The kinds of models that have been devised to explain the relative abundances of the species in an area show a similar type of dichotomy. One kind may be called "resource apportioning models"; such a model is constructed by postulating the way in which coexisting species subdivide among themselves some necessary resource which is assumed to be the limiting factor (and the same limiting factor for each species present) that sets a limit to each population's size. Three resource apportioning models are the **Niche Preemption Model**, the **Broken Stick Model** and the **Overlapping Niche Model**. The first two predict a community's ranked-abundance list while the third predicts a community's species-abundance distribution.

Models of the second kind are called "statistical models". They consist of assumptions about the probability distributions of such variables as the numbers of individuals of each of several species in a given area, and their predictions are expressed as species-abundance distributions. Three examples of statistical models are the **Truncated Negative Binomial Distribution**, the **Logseries Distribution** and the **Lognormal Distribution**.

The resource apportioning models are conceptually nice, but not practical in the real world. Rarely do we have the time and money to determine and measure all habitat variables and determine if one and only one limits the population sizes of every species present. Besides, even if we did have all the time and money we wanted, almost certainly we would find different limiting factors for each species present.

The statistical models are much more comfortable to use. The hypotheses constituting each model are assumptions about probability distributions. Because these are non-normal (also known as non-parametric) probability distributions they are intuitively more likely candidates for practical use. I promised that I would not go deeply into mathematics today, because I do not want you to fall asleep or have your eyes glaze over, but I must include this explanation. The two hypotheses that give rise to the negative binomial distribution are that the numbers of individuals in the several species in a sample are a Poisson variate, and that these have parameters that are themselves random variates from a gamma distribution. Details will not be given, but the point is that the model is couched entirely in the language of mathematical statistics. It says nothing about the ecology of the species, their environmental tolerances, and whether

(and if so how) their abundances are limited by shortages of resources and by competition.

Therefore, if a model of this kind fits empirical data, the only conclusion that can be drawn with any confidence is that the probability distributions underlying the model have indeed the forms postulated, at least approximately. But, this conclusion is not any less mathematical, or any more ecological, than the assertion that the model fits the data. The last step of arguing back from acceptable statistical hypotheses to acceptable ecological hypotheses still remains to be done. It is usually the most difficult step in an investigation of species abundance relations and no one has succeeded at it. At least, not so that everyone feels comfortable.

Given all the limitations, cautions and hesitations expressed above, you may well ask if there is anything to be gained by fitting these models to empirical data? The answer is, "yes". In the practical, applied world in which we live and work, the fitting of statistical distributions to empirical data leads to economy of description: a large mass of data can be summarized by naming the distribution that fits it and giving the estimated parameters of the distribution. This obviously facilitates comparisons among different communities. In addition, we can use parameter-free distributions when our data are less than ideal. All of these conditions typically apply to aquatic ecosystems and, quite often, to terrestrial ecosystems.

Back in the early- to mid-1980s, before I became aware of geographic information systems and spatial statistics, these statistical models were the best tools I could find. After looking into the mathematical assumptions and rigor to apply to the comparison of communities of lotic macroinvertebrates, I finally opted for testing the logseries distribution and found an extension that addressed the problem of relating the distribution to ecological factors. This extension was Mountford's similarity index that is based on the logseries distribution and can be clustered. This similarity index also has the desirable properties of being fairly insensitive to sample size than other such indices and decreasing in value with fewer species at each site while increasing with more common species. Clustering is a technique that permits us to visually assess how close or distant are different sites where samples are collected.

Toward the end of the section on diversity indices I mentioned the problem of mixed taxa. This is a problem with any statistical model, too. In my opinion it comes from the all-too-common practice of collecting data without sufficient regard to where, when, how and – most importantly – the analytical methods to be applied to the results. If you want to use a statistical model, you need to understand in what form the input data must be. Then you know to do your sampling during the time of the year when you can identify every organism to the species level. The alternative is to report all results at the level of genus or family. Any taxonomic level is acceptable as long as everyone knows what it is and the interpretations take the taxonomic level into account.

From the post-doctoral research I conducted using data from rivers and streams all over Idaho, and collected over a large number of years, I was able to discern patterns that could be tentatively given ecological meaning. The data

were not collected with this analysis in mind, so the problems of mixed taxa, collection methods, collection timing and all other variables were totally uncontrolled. Yet a conservative interpretation showed similarities that appeared to be closely correlated to habitat type regardless of location within and between river systems. In retrospect, I still think it was a good contribution for the times. Now, however, my knowledge and insight are much greater and I want to share this insight with you.

Modern Solutions

The problem with diversity (or biodiversity) is that it does not answer the question of why we find the organisms we do, in the relative abundances we see, in a particular area. The diversity indices and statistical models go only just so far. The key step is interpreting the data we have collected and giving it ecological meaning. This critical step, I suggest to you, can best be accomplished by the application of spatial statistics and spatial analyses using a map algebra within a geographic information system (or GIS) and by the quantitative modeling of uncertainty and subjective variables using fuzzy sets and fuzzy system models.

The most important attribute of biological or ecological data is not how much, but where. Just ask any hunter or fisherman the first question he would ask when told the prospects for success are high. Invariably, the answer is "Where are the ... " deer, elk, salmon, bass or other animal of interest. Before the almost-universal availability of high powered computers and sophisticated GIS software, this tool was not available to the field biologist and ecologist. Now, however, we have no excuse not to use it.

Whether we are preparing an environmental assessment for a proposed mine, assembling a compliance report or documenting revegetation efforts for reclamation bond release purposes, there is little information in knowing that the average number of individual plants or animals is a certain value. We know that the environment varies across the site, so the distribution of organisms will not be uniform. Figure 1 illustrates how we can interpolate point sampling data into a 3D surface that immediately imparts a large volume of information about the organisms in question.

Going beyond this type of analysis and mapping toward what I suggest be done is illustrated in Figure 2. This shows how the Istituto Trentino di Cultura (ITC) used a GIS to associate alpine wetland diversity indices (species richness) with other environmental factors. The project's goals were to assess the "biodiversity hotspots within a network of biotas in Trentino" and analyze "the ecological structure of the biotas for modeling the species richness". They used an algorithm that appears to produce a resource-allocation statistical model, with all the shortcomings of this approach. But, to help interpret the results, they applied spatial analyses to associate the calculated values with measures of land use, isolation and human disturbance.

The informational value of mapping the distribution of values rather than

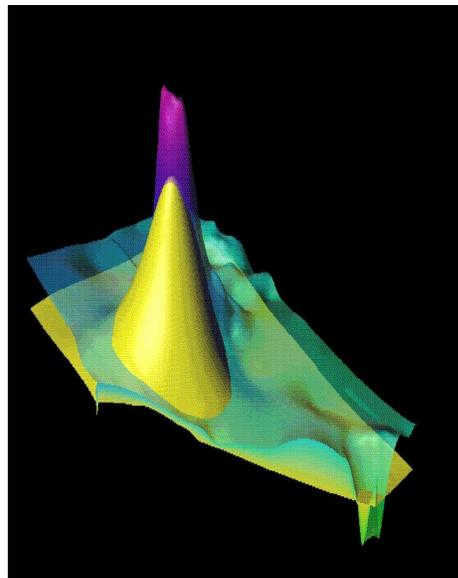


Figure 1: An interpolated surface that could represent the distribution of certain species of plants or animals across a given area. This is much more useful information than seeing the average number of individuals located there.

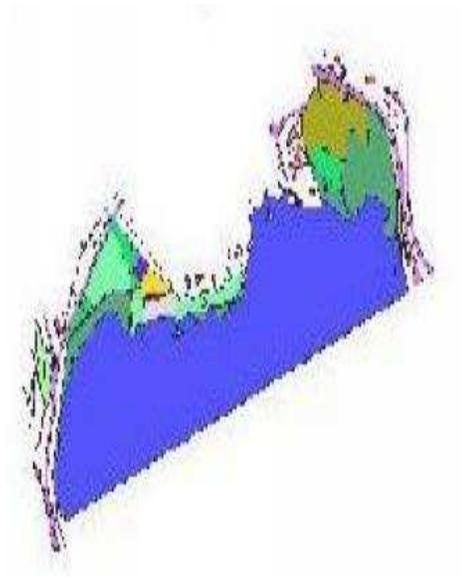


Figure 2: Mapping the associations among calculated species richness values and the physical factors for wetlands adjacent to an alpine lake in northern Italy.

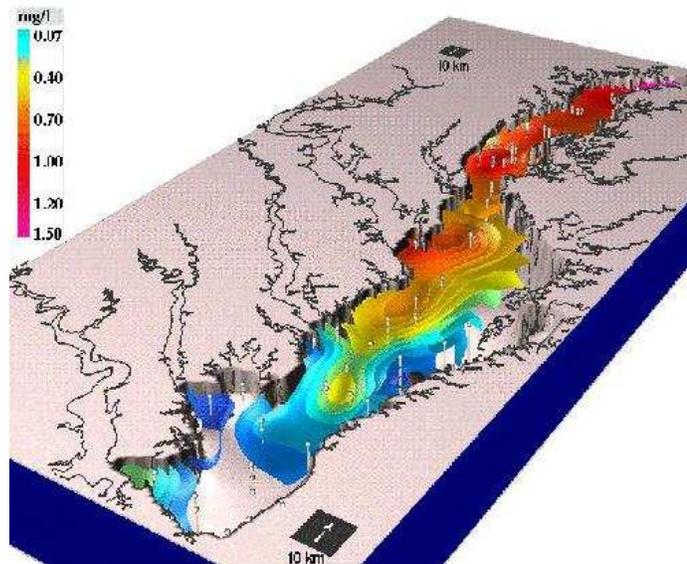


Figure 3: Distribution of cadmium within a river reach. Notice that concentration levels can be seen relative to depth and longitudinal position. Sampling points indicated by vertical lines.

reporting summary statistics such as the mean and standard deviation is instantly apparent in Figure 3 from the GIS Modeling Laboratory at the University of Illinois. While this map shows chemical concentrations in a river, the same process can be applied to plants or animals distributed throughout an “Existing Environment” in an EIS or a reclaimed mine site.

You’ll notice that the concentration is much higher at the upper end of the map (we can assume that is the vicinity of the source), and by the time the chemical has dispersed longitudinally downstream and vertically with river depth the concentration drops. It is so much more powerful to use analytical results presented as maps rather than as tables of numbers when making management decisions that it should become a standard for assessments of every type.

This type of analysis is one alternative to the use of diversity indices or species-abundance models as statistical functions. Here, we are approaching the underlying goal of explaining why we observe the organisms we do in a particular area and why two areas may differ in their species populations. Another illustration will lead us to the analysis of function within ecosystems as the more important consideration. Ecosystem structure, particularly of the biotic component, is a reflection of the underlying function without being the complete explanation. More on this shortly.

This next example, also from the ITC in Italy is a spatial analysis and mod-

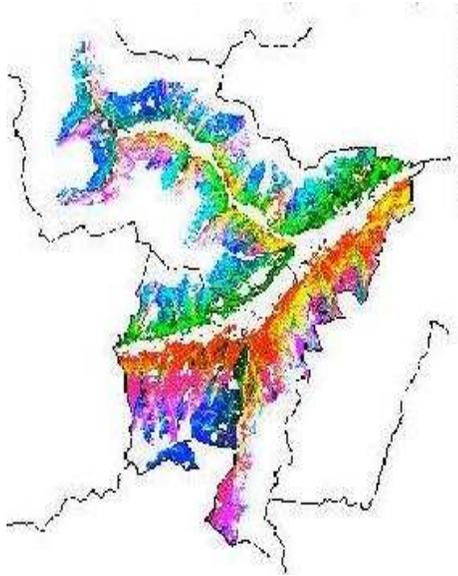


Figure 4: Pilot study area classified according to elevation, aspect and slope. The resulting 18 classes have been ranked for desirability as monitoring sites.

eling of deer browsing damage to regenerating forests (Figure 4). Within the Trentino area, roe deer populations increased from 5,350 deer in 1965 to 25,210 deer in 1994 while red deer increased from 200 in 1970 to 3,893 in 1994. Because of this herbivore population increase, the risk of impacting forest composition and dynamics had to be assessed.

The study design is to identify monitoring sites based on elevation, slope and aspect, then collect data on damage type and intensity. Figure 4 shows the microclimate variation, vegetation zones, and 16 subregions. These data will be used to establish monitoring sites and correlate the results with environmental variables. It will be very interesting to learn how these environmental variables affect the distribution of roe and red deer populations within each of the subregions.

The concept of species diversity was useful to focus thinking on the distribution of plants and animals and to try to summarize all the complex environmental factors of place and time into a single number. Today, we have the tools and knowledge to characterize ecosystems, regions, mine sites or any other area from a small yard to the entire Earth in more scientifically substantial, practical, and meaningful ways.

Rather than looking only at structure (that is, the plant and animal species in the area of interest) we should look at function: energy flow, nutrient cycling, and paths of change. The natural world is highly dynamic and diversity is analogous to any other data collection: a snapshot in time and space that is

disconnected from the dynamic nature of ecosystems.

The eruption of Mt. St. Helens in southwestern Washington in May 1980, the massive fires in Yellowstone National Park in northwest Wyoming in 1988, and the revegetation of a mine site, waste rock pile or tailings pond established on physically and chemically disturbed soils all represent the beginning of very dynamic changes. The biodiversity, species diversity, or any other structural index you want to apply to these areas will start off very small but increase very quickly. Unfortunately, diversity indices are not ratio data, that is, the difference between 1.0 and 2.0 is probably not the same as the difference between 2.0 and 3.0. Statistical models of species abundances say nothing about the rate of change or the nature of the changes. It is time we stop looking at natural ecosystems as static and unvarying. We can measure the amounts and rates of change using time-series analyses in a GIS. The insight we gain from this information is much more useful in making management decisions than is a static measure of dubious scientific value.

Another feature of the natural world that could not be accommodated until the recent past is the inherent uncertainties in the objects we observe. The words we use to describe this uncertainty are all subjective. We describe slopes as being "steep", of the topography being "gently rolling" of population size being "large", and so on. We all know exactly what these terms mean to us. But, they can mean different things to different people.

Now, however, we have a system of mathematics that permits us to quantify these subjective terms and manipulate them with provable rigor. Developed by Lotfi A. Zadeh in the mid-1960s, this system is called fuzzy logic. The inherent uncertainty in the world is captured in fuzzy sets, manipulated according to the rules of fuzzy logic then translated back into a possibility value (not probability, possibility) that is a measure of the relative risk of a certain outcome. The sets and logic can be assembled into fuzzy system models that are analogous to expert systems. These tools can be applied to large, natural ecosystems as well as disturbed ones and can be used to gain insight into their dynamics and to predict future states. Given all the tools, techniques and analytical systems we now have available, there is no more value to looking at diversity (or biodiversity) as a indicator of anything. When you are feeling ill and go visit your physician, you would probably be terribly disappointed if all she did was take your temperature before issuing a diagnosis and prescribing a cure. And, if the cure involved blood-letting or enemas you would be justified asking about her qualifications as a physician when it is your body at risk. Diversity may still be a nice concept that evokes warm, fuzzy, visceral responses among the less informed, but it no longer has a place in the modern applied environmental sciences.

Conclusions

Multivariate spatial statistics (also called geostatistics), map algebra (tools for mathematically combining data layers within a GIS), and fuzzy system models

that quantify subjective and linguistic variables permit us to rigorously analyze complex ecosystems and extract useful information that managers and policy makers can effectively use to create knowledge and make informed decisions. The simplifications and problems in applying theory to the real world when using diversity measures can safely be put aside.

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