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SPECIES-BASED VEGETATION MAPPING:

AN EXAMPLE FROM THE GRAND CANYON

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ABSTRACT

Data on plant species occurrence produced during vegetation monitoring and mapping efforts are often unavailable for mapping of plant distributions at the species level. Although maps of plant associations and permanent plot data are important tools for park management, these end products are not suitable for many needs. But, the species-specific data produced during these projects can be valuable assets when compiled into larger databases and made available for unanticipated uses. This is required as studies of the distribution of individual species in both time and space repeatedly emphasize the transient nature of plant associations. Using the distribution of Utah Agave *(Agave utahensis*) in the Grand Canyon as an example, this chapter illustrates how data can be compiled and applied to management and scientific issues using a database constructed from raw field data. Coordinated efforts should be undertaken to compile, archive, and distribute available species-based data. The creation of a virtual vegetation map of species-based distributions is suggested.

INTRODUCTION

National Parks and other land management units have pursued the important goals of: 1) Developing vegetation association maps for use in Geographic Information Systems (GIS) (http://biology.usgs.gov/npsveg/index.html) and, 2) Establishing permanent vegetation plots as a baseline for monitoring change. These two goals are essential for many uses, but the information produced during the identification process on the occurrence of individual species is not always viewed as important enough for retention and distribution. These data, especially relevés sampled during the association mapping and ground-truthing processes, are indispensable for understanding plant distributions at the species level.

A relevé is a ground plot that provides a plant species list from a homogenous area of predetermined size, with estimates of the coverage of each species (Mueller-Dombois and Ellenberg 1974). Although originally intended to be a fairly complete listing of species within a plant "community", this method has been abbreviated to record only a handful of dominant trees and shrubs for use in ground checking maps of plant associations developed from remote sensing. The data from each relevé are far less quantitatively rigorous than those from a more intensively measured vegetation plot, being quickly estimated rather than actually measured. But because less time is required to record each plant, tens of relevés can be completed in the time required for each quantitative vegetation plot or transect. If a study requires measurements across a large and varied landscape, the relevé method can better represent this entire range of spatial variability than will a much smaller number of more detailed plots. For example, if a landscape contains 50 unique combinations of species, 100 relevés will encompass more of this variability than will 20 highly quantitative random plots.

Flexible Classification Systems

Vegetation maps are almost always based upon plant communities or associations defined by one to several dominate individual species. Alternatively they can be characterized by a

vegetation structure or growth form (grassland vs. forest), or even a soil or hydrological condition (rock outcrop vs. wetland). These classification schemes are essential for lumping what are distinct, yet similar, microhabitats to create mapable units. Without these simplified units, polygons could not be developed to make up the final GIS map. Although vegetation maps are essential for many purposes, the near-exclusive focus on the plant community or association concept leads to misconceptions about the nature of plant species distributions. This is especially true of efforts to create regional or nation-wide vegetation maps using standardized classification schemes. While a standardized classification system is essential for regional and inter-regional comparisons, it may not be the ideal system for particular needs within an individual park unit.

No single classification scheme serves all purposes for a vegetation map. For example, in 1986 one of us (Cole) participated in vegetation mapping and classification at Indiana Dunes National Lakeshore. The fire ecologist developed a scheme emphasizing fire frequencies, while the wetland ecologist developed a scheme based on flood frequency and depth to water table. Both schemes were valid, and each served certain National Park Service management needs. A compromise classification was eventually developed that was sub-optimal for either fire or flood management planning. What was not evident at that time was that vegetation maps need not exist solely as fixed paper entities. Once in digital form, any hierarchical classification system can be re-formulated to best address the issue at hand, providing that the base-level raw data remain available.

Most of the polygons mapped in the Indiana Dunes project were consistent from one classification scheme to the next. That is, the placement of polygonal boundaries was independent from the specific association classified within that polygon. Thus, the hierarchical classification of associations was a secondary characteristic of the map that could be flexible. The primary characteristic of the map was the spatial orientation and boundaries of polygons representing fairly homogenous habitat areas. A map that efficiently represents homogenous vegetation units can be re-classified in many different ways, providing that the base-level raw

data remain available for later use. This is especially true in the arid west, where plant distributions are usually controlled by such polygonal features as geologic substrate, elevation, slope aspect, and slope angle. Thus, the raw data on occurrences of individual species, obtained during the mapping process, are just as important as the mapped polygons. Without these raw data, the map polygons cannot be reclassified for unanticipated future applications.

Individualistic vs. Community Ecological Models

Vegetation can be viewed as an assortment of individual species, each distributed according to specific environmental requirements (Gleason 1926), or alternately, as groups of species clustering together in larger ecological community, association, or biome units (Chronquist 1916). The latter view has worked well for characterizing vegetation across large regions, where the complex individual distributions of innumerable species would defy understandable classification and summarization. This community-based approach also works well where one or several species so modify the microhabitat that they are usually found with associates requiring this modification. An example of this type of relationship would be shade loving species that only occur under a closed-canopy forest.

But these community concepts have limited utility in understanding the geographic range of a species, especially in open-canopy, arid to semi-arid systems. In a series of studies of plant species distributions along environmental gradients, Robert Whittaker (and many others) have demonstrated that species are usually distributed according to the environmental tolerances of each individual species, rather than in associated groups (Whittaker 1951; Whittaker and Niering 1965, 1968a, 1968b; Shippley and Keddy 1987; Bastow and Allen 1990). That is, the distribution for most species is independent of the distributions of other species; they rarely form reliable associations. Species occur along environmental gradients and are typically the most abundant near the central point of their range of tolerances. This concept has become the accepted model in plant ecology. For example, Begon et al. (1990; page 620) state: *"There may be communities that are separated by clear, sharp boundaries, where groups of species lie*

adjacent to, but do not intergrade into, each other. If they exist, they are exceedingly rare and exceptional." Yet these "*exceptional*" boundaries are precisely what is displayed along every polygon edge on a plant association map.

The notion of each species independently distributed according to its unique tolerances is often referred to as the *"continuum concept*" due to its view of the habitat as a gradually changing range of continuous variables rather than homogenous patches with discrete boundaries. The continuum concept is so well accepted by plant ecologists that it has passed beyond the testing stage and is instead the focus of refinements such as how to best mathematically represent the response functions of species along environmental gradients (e.g. Oksanen and Minchin 2002). Thus, the simplified community or association classifications used in most vegetation maps cannot be used to portray the ranges of individual species, except perhaps the dominant species for which the communities are named.

The difficulties in using a community-based map to describe a species range can be demonstrated with the use of Pinyon-Juniper Woodland (P-J) on the Colorado Plateau. This association is one of most recognized of all western plant associations, but it has little meaning in terms of species composition of even of its dominants. Throughout the range of P-J it can contain one, but frequently neither, of two pinyon species (*Pinus edulis, P. monophylla*), which share the range with one (or none) of several different juniper species *(Juniperus californica, J. osteosperma, J. monosperma, J. deppeana, J. occidentalis*). Although other species may locally co-occur where these pinyons or junipers grow, there is probably no other plant species that conforms to the range of pinyons and junipers, aside from the species of mistletoe that infect them.

Rather than being a homogenous ecological unit, the P-J is perhaps better thought of as an entity visually recognizable to humans as small to medium sized dark green conifers, typically occurring at mid-elevations. As a term, P-J is useful for communication of human perceptions,

but it does not necessarily convey much ecological meaning outside of a local area. P-J is more effectively understood as a general geographical term, much like "desert shrubland" or, "montane forest". Unfortunately, the highly visible nature of these dark colored conifers on a bare landscape, especially in aerial photographs, has led to the widespread impression that the P-J is an important ecological entity, homogenous from top to bottom, and from range to range. Studying aspects of the P-J using a vegetation map, such as plotting seed availability for the Pinyon Jay *(Gymnorhinus cyanocephalus*), becomes a impossible exercise in guessing which parts of the P-J actually contain "P" rather than just "J".

The individualistic or continuum model of species distributions is further supported by the study of past vegetation change. Over the last 20,000 years, plant species migrated as individuals, rather than identifiable associations (Jackson and Overpeck 2000; Foster et al. 1990). These results are particularly evident in records of plant macrofossils from fossil packrat middens (Cole 1982; 1990), which allow the identification of individual plant species from specific locations in the past. These records demonstrate that the modern associations we use as ecological units are highly ephemeral entities. The record of change through time at any one locality is analogous to moving along a contemporaneous environmental gradient through space. Individual plant species appear or drop out as environmental tolerances for those species are met or exceeded.

Individualistic shifts of plant species are not restricted to ancient periods or even the historic past. This is how on-going changes in plant distributions are described; as a change in the distribution of a particular species. Plant mortality during a drought is described as the death of an individual species, and almost never as a shift in plant associations. A plant invasion into a new area is described as an increase in that particular species, not as a change in plant associations. Using the P-J example, studies have shown that when these species increase or decrease, the shift usually involves just one or the other, and many times the pinyon shift in the opposite direction of the juniper. For example, although overgrazing is widely believed to lead

to range invasions by P-J, recent packrat middens from Capitol Reef National Park in Utah record an increase in only juniper, and a decrease in pinyon with grazing (Cole et al. 1997). Fossil pollen from the Verde Valley of Arizona show that juniper increased during the last 100 years, while pinyon remained stable (Davis and Turner 1986).

These results imply that maps of plant associations are inappropriate tools for measuring vegetation change (Davis 1989). A radical change in even one of the two dominant trees of the P-J (pinyon or juniper) would be difficult to detect using an association map. Detecting a change in a shrub or herb species would be impossible. We should expect the constituent members of associations to continue to respond in different ways, just as they have during the past and present.

Species-Based Vegetation Mapping

Plant species are the most stable entities for mapping vegetation. Despite continuing disagreements among plant taxonomists, and the gray areas caused by hybridization and ecotypes, species are scientifically well-documented and defined. Even though the taxonomic rank of an individual species may undergo periodic shifting through splitting and lumping, it usually remains an identifiable entity, perhaps continuing as a variety or species-complex, if not a species. In contrast, definitions of associations, communities, and formations will change between times, classifier, and regions. These definitions, usually defined by one or a few dominant species, are not suited for monitoring change in the secondary plant species. While these secondary plant species may not individually dominate the community in terms of coverage or abundance, they nevertheless can be critical components of the habitat.

Despite the utility of the species concept, the spatial distribution of individual species are typically poorly documented in western North America. Almost all state floras report distributions only by county of occurrence. Although many herbariums are currently digitizing

their collections and making them available on-line, they are using the county as their spatial unit. These county records are adequate for states with many small counties spread over homogenous landscapes. But they are particularly poor for use in western states where counties can be larger than entire northeastern states, and the range of climatic conditions within a mountainous county can exceed the range found within an entire region of several more homogenous states. County-based records are particularly problematic for parts of California, Oregon, Arizona, New Mexico, Nevada, Utah, and Wyoming.

There are some exceptions to this paucity of data on individual species distributions. For example, Turner et al. (1995) published an atlas of 414 species ranges based upon 100,000 records of occurrence within the Sonoran Desert (http://wwwpaztcn.wr.usgs.gov/atlas/). This atlas, compiling 30 years of field observations, has no peer elsewhere in the western United States. Clarlet (1996) maps the locations of herbarium collections for 24 species of conifer in Nevada. The Southwest Exotic Mapping Program (SWEMP) (http://www.usgs.nau.edu/SWEPIC/swemp/maps.html) also uses an individualistic approach in plotting the occurrence of weed species, rather than attempting to assign them to association types.

The most unfortunate aspect of this sparse information is not that the data have not been collected, but rather that the data have not been synthesized and made available for widespread use. Individual scientists who have conducted field investigations have little incentive to expend the considerable effort in editing their raw data to make it available to other scientists. who are their potential competitors. Large agencies that have collected data for other uses often have barriers to open data sharing. For example, the U.S. Forest Service Inventory and Analysis Program's (http://fia.fs.fed.us/) target is to sample one site for every 6000 acres of forest every 5 years. Although these data have recently become available at the county and plant association level, information on occurrences of species and vegetation change are still not available even to most scientists within the U.S. Forest Service itself. Research projects coordinated through the

USGS GAP Analysis Program (http://www.gap.uidaho.edu/) have used data from tens of thousands of relevés to classify and assess vegetation maps, but these raw data were never considered to be products and are not generally available except to the original project investigators.

In contrast to the above, the NPS-USGS vegetation mapping program (http://biology.usgs.gov/npsveg/index.html) has fortunately made detailed vegetation plot data available for the parks that have been completed. VegBank, an effort of the Ecological Society of America (http://vegbank.org/vegbank/index.jsp), is an important continuing effort to compile plot data, but so far contains data from relatively few plots.

Species-based mapping efforts will not replace either permanent monitoring plots or plant association (land cover) maps, both of which fill critical needs. But plot-specific data produced in by these other efforts can be included in spatial databases for individual species. Table 1 summarizes some of the strengths, weaknesses, and features of these three approaches to plant monitoring.

Table 1. Three different types of spatial vegetation data and their uses.

	Plant Association Map	**Species Occurrence Data**	**Permanent Vegetation Plot**
Coverage Type	Polygon coverage	Point data that can be used to model polygonal distributional rangemaps.	Usually point data
Primary Use	Analyzing/Comparing areas of different habitat type	Documenting distributions of and co-occurrences of individual species	Documenting current resources and vegetation change
Strengths	Classifies entire landscape. Simplifies vegetation into convenient units.	Essential for use in studies of individual species. Can be used to re-classify association map for unanticipated needs. Ideal for use with well distributed threatened and exotic species.	Can be a convincing documentation of change, especially when combined with replicate photographs. Ideal for monitoring change with specific populations of threatened, endangered, and exotic species.
Weaknesses	Assumes that species co-occur in associations through time and space. Allows only the one classification scheme anticipated by the authors. Statistical analysis of change impossible.	Data is rarely collected in a systematic manner making local statistical analysis problematic.	Time consuming sampling procedures produce too few plots to statistically characterize entire spatial variability of landscape. Statistical analysis complicated by the pseudoreplication problem.
Location Accuracy	Mapped polygon boundaries may be misleadingly accurate due to the random diffusion of species across association boundaries.	Variable, depending upon the mapping and technological resources of the scientists.	Highly accurate. Hopefully documented on the ground at each plot.
Taxonomic Accuracy	Poor (Association Level). Assumes constant associations in time and space.	Detailed (Species level observations)	Precise (Species, subspecies, or variety level with voucher specimens)
Optimal Spatial Extent	Medium Range; the size of the management unit being mapped.	Large; possibly the entire range of the species.	Small; hopefully characterizes entire landscape, but more likely only characterizes area within plot.

APPLYING SPECIES-BASED DATA:

AN EXAMPLE FROM THE GRAND CANYON

Between 1978 and 1981, 1420 plant relevés were sampled throughout Grand Canyon National Park (GRCA) to produce a vegetation map (Warren et al. 1982). An additional 130 relevés surveyed by Kenneth Cole (1981) in a gradient analysis of individual species distributions were added to that total and are included in the Warren report. These relevé data were especially valuable as many had been collected from remote locations where water is unavailable. The collectors did extensive hiking, sometimes starting from remote helicopter landing sites. Since that time, helicopter access within the GRCA wilderness of has become much more sensitive and expensive. These relevé locations can still be reached without mechanical assistance, but only at tremendous expense in time, logistics, and safety. Thus, these Grand Canyon relevé data are a highly valuable asset.

Warren et al. (1982) used relevés and aerial reconnaissance data to produce an excellent vegetation map, applying the vegetation classification system of Brown et al. (1979). Although this review may seem unfavorable for the map compiled by Warren et al. (1982), our criticism applies only to the plant association paradigm mandated for the mapping effort, not to the data themselves, or to the field effort.

In 1998, we became interested in analyzing the GRCA relevés to estimate the climatic tolerances for individual plant species for a USGS paleoclimatology project. Unfortunately, the final vegetation map only displayed plant associations classified according to the Brown et al. (1979) system. The problem was not in the system itself, but with the underlying assumption that individual plant species were constrained within any association. We needed the raw, unclassified field data from the relevés in order to extract the distributions of individual species. The FORTRAN punch cards containing these data had been discarded long ago. After several years of searching, Peter Warren was able to locate photocopies of the original field data sheets

and he generously made them available for our effort. We entered the field data into a relational database for use in GIS.

Utah Agave within the Grand Canyon

Utah Agave (*Agave utahensis*) is one of the most common plant species within the Grand Canyon. We will use it to demonstrate an application of species-based data. Although Utah Agave it is a very distinctive plant, it is too small (30 to 60 cm broad) to have been incorporated in remote sensing mapping efforts. Utah Agave is an important food source for many species, especially packrats. Packrats require succulent plant food (at least 50% water by weight), often *Juniperus, Opuntia*, or *Agave*, to supply them with adequate moisture (Vaughn 1990). Packrat populations, in turn, can affect the populations of other species, such as rattlesnakes (Repp 1998). Utah Agave was also an important food source of Nnative Americans, as evidenced by the abundant agave roasting pits distributed over the Tonto Platform of the Grand Canyon. Thus, the distribution of this fairly insignificant plant species has implications for mammalogists, herpetologists, and archaeologists, as well as for botanists and paleoclimatologists.

Because Utah Agave could also be an important indicator of climate, it became of interest to the USGS Global Change program. During the ice ages, Utah Agave distributions fluctuated in elevation from the bottom to the top of the Grand Canyon. So, understanding the modern distribution of Utah Agave was essential to understanding past climate change. We produced a rangemap for Utah Agave (Figure 1) through a compilation of all available records (Cole et al, 2004). These GRCA relevé data were invaluable in defining its eastern distribution. We discovered that its upper range limits are controlled by minimum winter temperatures. This information then allowed us to use past Utah Agave distribution as an indicator of paleoclimates (Cole and Arundel, In Press).

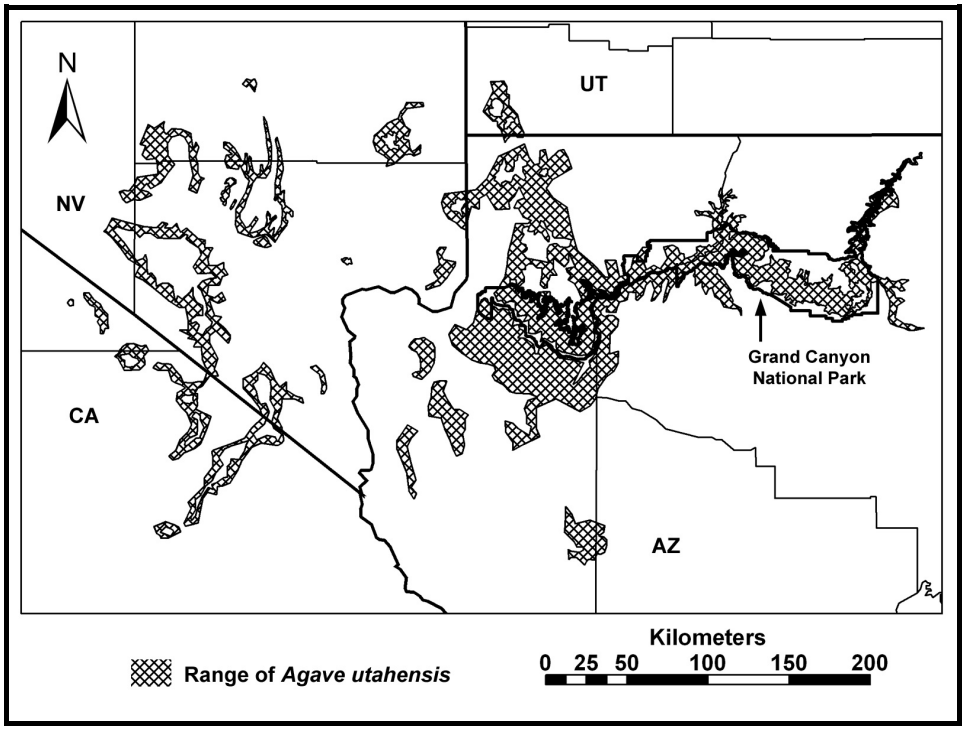

Figure 1. Entire geographic range of Utah Agave modeled using data from the Grand Canyon relevé database, a Digital Elevation Model, herbarium records, published regional estimates of elevational range, and field experience of several regional specialists.

The vegetation classification produced by Warren et al. (1982) includes Utah Agave in the name of only one of 63 associations; the Snakeweed-Mormon Tea-Utah Agave association (153.11011) (Figure 2). But, Utah Agave actually occurs in only 61% of the relevés obtained from areas mapped as this unit. From this, one might conclude that Utah Agave is only an occasional species within the canyon. But the relevé database shows that Utah Agave actually occurred in 360 (35%) of all eastern Grand Canyon relevés, and was listed as occurring within 27 (43%) plant associations (Warren et al. 1982). Thus, even though it was not found in many of the relevés named for it, it is one of the most widely distributed species within GRCA.

The Snakeweed-Mormon Tea-Utah Agave Association is an association of exclusion rather than inclusion. All three plant species, Snakeweed, Mormon Tea, and Utah Agave, actually grow throughout the Grand Canyon and are not particularly more abundant within any one particular association than elsewhere. But, they had been selected to typify the association of extremely

arid, barren rockscapes because little else can grow there. That is, the environment on these low elevation rockscapes is so stressful that only these three extremely well adapted species remain; most other species are excluded.

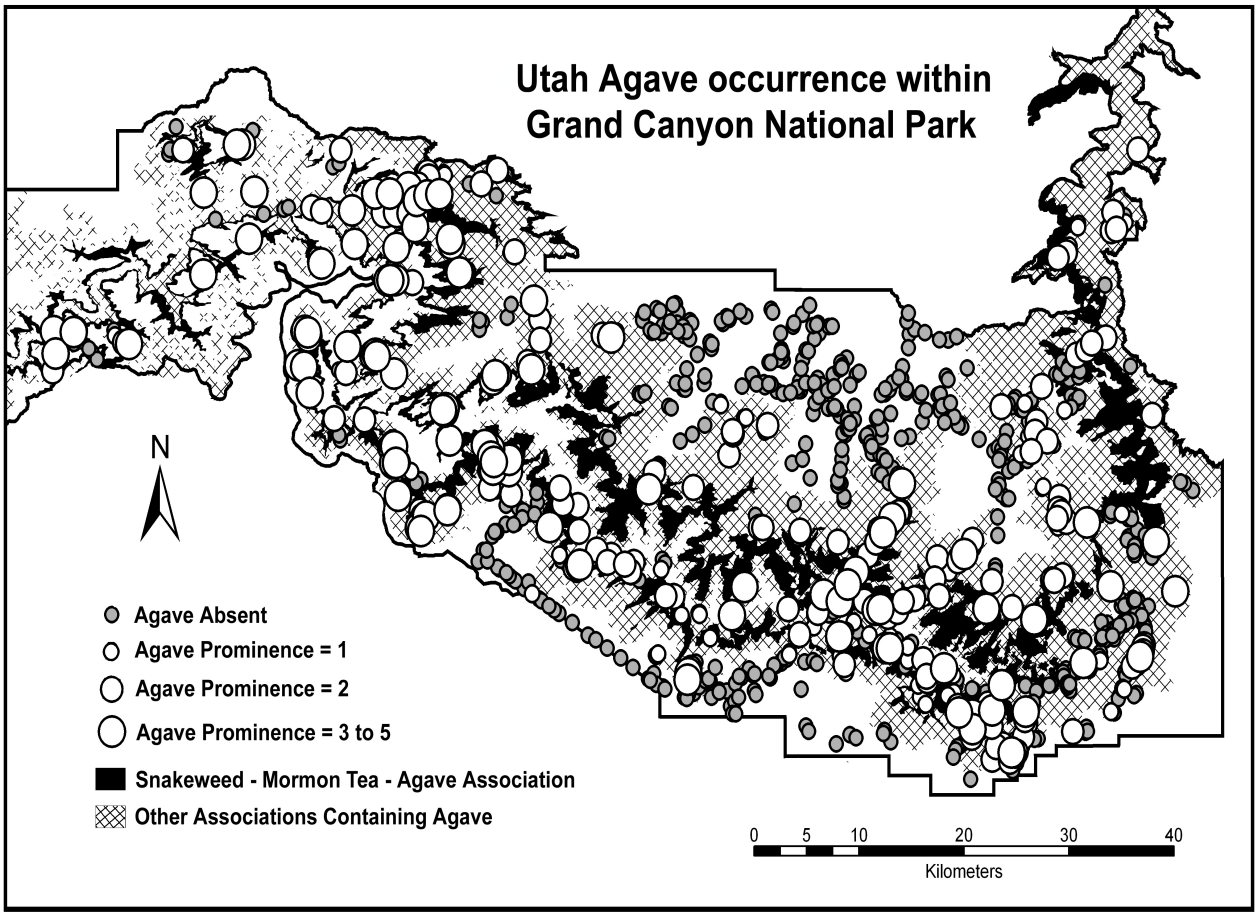

Figure 2. Map of Utah Agave records within the eastern Grand Canyon showing: The actual presence and absence data for *Agave utahensis* in the eastern Grand Canyon using data from 1200 relevés from the GRCA database; the distribution of the Snakeweed-Mormon Tea-Utah Agave Association, and; the mapped distribution of associations in which *Agave utahensis* is a "Characteristic Species" or "Associated Species". Associations where Utah Agave is an"Ocassional Species" are not mapped.

Utah Agave occupies an extreme range of elevations. Phillips et al. (1987) gives a range of 366 to 2195 m (1200 to 7200 feet), whereas the Warren et. al. (1982) database records it in relevés from the lowest relevé at 427 m to 2438 m (1400 to 8000 feet). Its frequency throughout this range can be estimated by calculating the percentage of relevés containing Utah Agave in

elevational classes (Figure 3). This analysis shows that Utah Agave is most abundant in the eastern Grand Canyon at middle elevations, between about 1000 and 2000 m elevation.

Table 2. Percent occurrence of Utah Agave in all plant associations that contain it in at least half of their relevés from the eastern Grand Canyon. Importance ranks for Utah Agave are from Warren et al. (1982). Percent frequency in relevés was calculated by overlaying the digital vegetation map with the relevé locations.

Plant Association	Importance of Utah Agave	Percent of Relevés
Scrub Oak-Snakeweed-Beargrass-Blackbush	Not Listed	83
Blackbrush-Pinyon-Juniper	Characteristic	78
Saltbush-Banana Yucca-Snakeweed	Occasional	67
Juniper-Pinyon-Mormon Tea-Scrub Oak	Characteristic	67
Pinyon-Juniper-Scrub Oak-Little Leaf Mtn Mahogany	Characteristic	65
Cottonwood-Brickellia-Acacia-Apache Plume	Associated	62
Snakeweed-Mormon Tea-**Utah Agave**	Characteristic	61
Juniper-Pinyon-Mormon Tea-Greasebush	Characteristic	61
Pinyon-Scrub Oak-Manzanita	Associated	61
Blackbrush-Mormon Tea-Banana Yucca	Characteristic	51
Mormon Tea-Big Galleta-Catclaw Acacia	Not Listed	50

Calculating the frequency of Utah Agave on different rock types reveals that it is concentrated on rocky substrates, especially limestone, sandstone, and shist (Figure 4). These data somewhat contradict the usual description of Utah Agave being abundant on limestone substrates (Gentry 1982). Although Utah Agave is frequent on limestone, it also is abundant on other steep rocky substrates with minimal soil. Because rock substrates with the highest frequency of Utah Agave are also those at middle elevations within GRCA, it is difficult to discriminate between elevational and substrate control of its distribution.

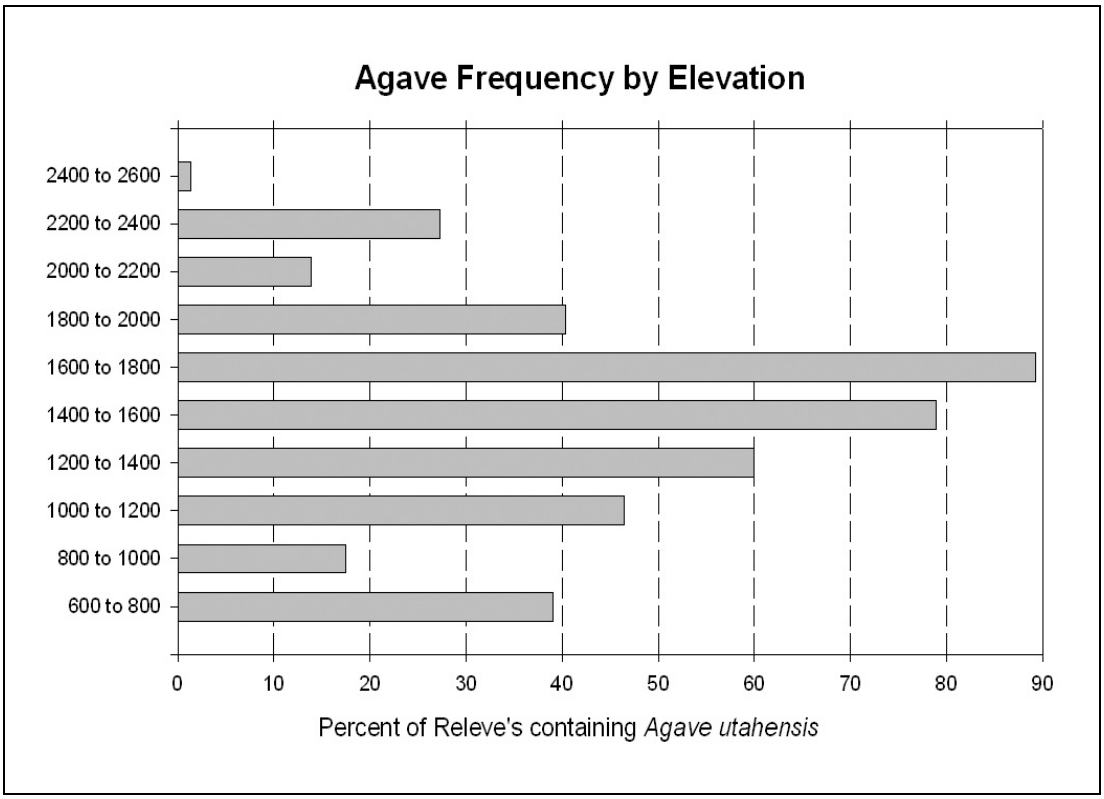

Figure 3. Distribution of Utah Agave within eastern Grand Canyon by elevation (m).

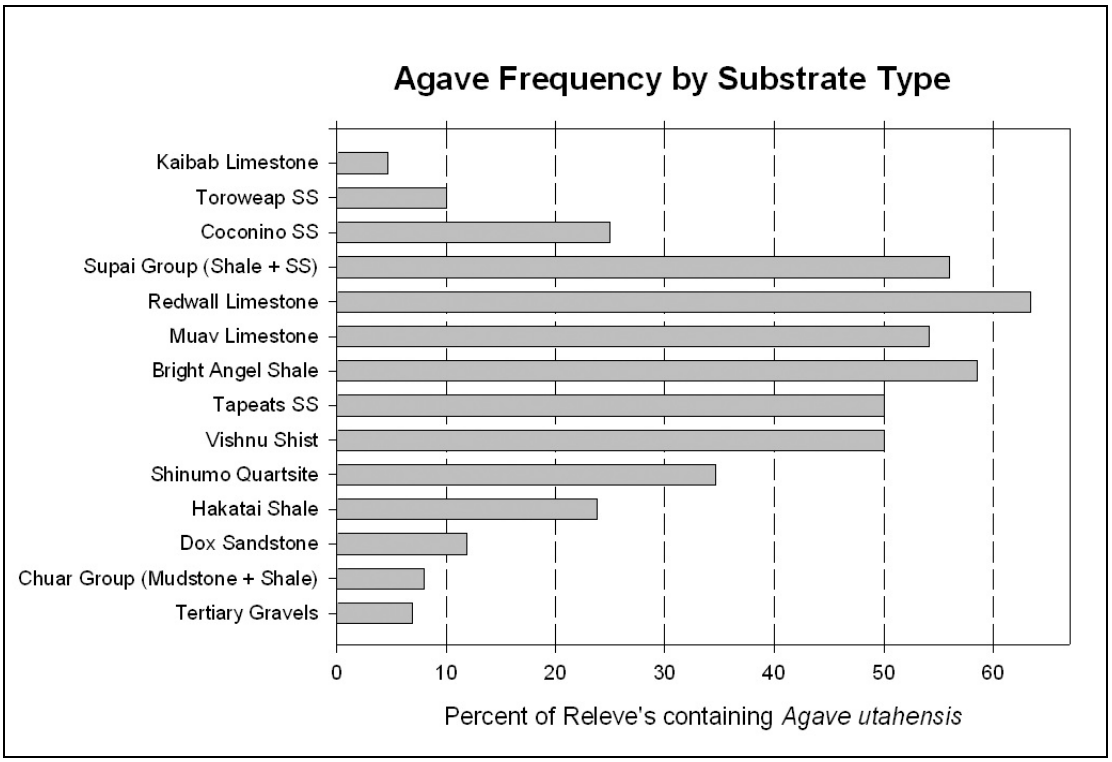

Figure 4. Distribution of Utah Agave in the eastern Grand Canyon by substrate type. Substrate types are shown roughly in elevational order as they occur within the canyon.

The distribution of Utah Agave within the Grand Canyon could be determined through the circular process of classifying and mapping associations, then creating a map of those associations known to contain Utah Agave. Although this approach is possible, it is entirely dependent upon the assumption that species limits co-occur along association boundaries, an assumption has been refuted in many studies. Applying this circular process to the Grand Canyon data of Warren et al. (1982) would map Utah Agave as growing up to 2680 m (8800') elevation where it occurs occasionally within the Douglas Fir-White Fir-New Mexico Locust Association. A check of the raw data reveals that the co-occurrence of Utah Agave in this association type was only around 1830 m (6000') elevation where fir and locust trees grow on north facing cliffs. The two highest documented occurrences of Utah Agave at 2438 m (8000'), within the Pinyon-Serviceberry-Gambel Oak Association, actually occur on exposed limestone cliffs within the canyon, rather than above the rim. Our site-specific analysis of Utah Agave reveals that it has substrate and thermal requirements much more specific than would be apparent from the association map. It is located inside the confines of the canyon rim where cloud formation is less frequent and the steep rocky slopes are open ground for stress-tolerator species (Grime 1979).

BUILDING A VIRTUAL SPECIES DISTRIBUTION MAP

The occurrence of Utah Agave in a relevé database was used as an example of how species-specific data can assist an unanticipated research project many years after data were collected. In this example, the raw field data were required for our effort. Any attempt to use the classified plant association map would have produced extremely misleading results about the distribution of Utah Agave. These same types of plot or relevé data could be used in projects involving any major plant taxa.

The techniques used here for Utah Agave could be applied to all the major plant taxa within an area, creating a true species-based vegetation map. This map would exist only as a virtual

(digital) entity as the polygonal boundaries circumscribing each species range would not necessarily coincide as they are forced to on an association map. From this virtual map, individual plant species could then be selected for inclusion on numerous printed versions. Such an approach, and its ability to generate customized maps, could be especially useful for informing land management decisions related to individual species distributions.

Creating species-based maps requires a re-ordering of priorities in vegetation mapping efforts. Ground-based observations such as relevés would be given a much greater emphasis as the focus shifted from spatial accuracy to taxonomic accuracy. Because only a few plant species can be identified to the species level from remote sensing data, such data would be less emphasized.

Species-based data collected as part of other efforts can be invaluable. The importance of these data should be recognized in their preservation and distribution. Coordinated efforts should be undertaken to compile, archive, and distribute available species-based data before such data are lost.

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REFERENCES CITED

Arundel, S. T. 2005. Assessing spatial models to establish climatic limiters of plant species' distributions. Ecological Modeling 182:159-181.

Bastow, J. and Allen, R. B. 1990. Deterministic versus Individualistic community structure: a test from invasion by Nothofagus menziesii in southern N. Zealand Journal of Vegetation Science 1: 467.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: Individuals, populations, and communities. Blackwell Scientific Publishers, Boston.

Brown, D.E., C. H. Lowe, and C. P. Pase. 1979. A digitized classification system for the biotic communities of North America, with community (series) and association examples for the southwest. Journal of the Arizona-Nevada Academy of Science, Vol. 14, supplement 1.

Charlet, D. A. 1996. Atlas of Nevada Conifers: A phytogeographic reference. University of Nevada Press, Las Vegas.

Cole, K. L. 1981. Late Quaternary vegetation of the Grand Canyon: Vegetational gradients over the last 25,000 years. Ph.D. dissertation, University of Arizona, Tucson.

Cole, K. L. 1982. Late Quaternary zonation of vegetation in the eastern Grand Canyon. Science 217: 1142-1145.

Cole, K. L. 1985. Past rates of change, species richness, and a model of Vegetational Inertia in the Grand Canyon, Arizona. American Naturalist 125:289-303.

Cole, K. L. 1990. Late Quaternary vegetation Gradients through the Grand Canyon. In, Fossil packrat middens: The last 40,000 years of biotic change in the arid west, J. L. Betancourt, P. S. Martin, and T. R. Van Devender (eds), University of Arizona Press, Tucson, AZ

Cole, K. L., Henderson, N., and S. Shafer. 1997. Holocene vegetation and historic grazing impacts at Capitol Reef National Park Reconstructed using packrat middens. Great Basin Naturalist 57: 315-326.

Cole, K. L., W. G. Spaulding, W. Hodgson, and K. Thomas. 2004. A digital rangemap for Utah Agave (*Agave utahensis*). Web document at: http//www.usgs.nau.edu/global_change/RangeMaps.html

Cole, K. L., and S. Arundel, In Press. Carbon 13 isotopic records from fossil packrat pellets reveal Younger Dryas cold period in Grand Canyon, Arizona. Geology.

Clements, F. E. 1916. Plant Succession, an analysis of the development of vegetation. Carnegie Inst., Washington.

Davis, M. B. 1989. Insights from paleoecology on global change. Bulletin of the Ecological

Society of America 70: 222-228.

Davis, O. K., and R. M. Turner. 1986. Palynological evidence for the historic expansion of juniper and desert shrubs in Arizona, U.S.A. Review of Palaeobotany and Palynology 49: 177-193.

Foster, D. R., P. K. Schoonmaker, and S. T. A. Pickett 1990. Insights from paleoecology to community ecology. Tree 5: 119-122.

Gentry, H. S. 1982. Agaves of continental North America. The University of Arizona Press, Tucson, AZ

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Botan. Club 53: 7-26.

Grime, J. P. 1979. Plant Strategies and Vegetation Processes. Wiley and Sons, New York.

Jackson, S. and, J. Overpeck. 2000. Responses of plant populations and communities to environmental changes in the Quaternary. The paleontological Society. 194-220.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley and Sons, NY.

Oksanen, J. and P. R. Minchin. 2002. Continuun Theory revisited: what shape are species responses along ecological gradients? Ecological Modelling 157: 119-129.

Phillips, B. G., A. M. Phillips, and M. A. Schmidt Bernzott. 1987. Annotated checklist of vascular plants of Grand Canyon National Park. Grand Canyon Natural History Association, Monograph Number 7.

Repp, R. 1998. Wintertime observations on five species of reptiles in the Tucson Area: Sheltersite selections/Fidelity to sheltersites/Notes on Behavior. Bull. Chicago Herp. Soc. 33: 49-56.

Shipley, B., and P. A. Keddy. 1987. The individualistic and community-unit concepts as falsifiable hypotheses. Vegetatio 69: 47-55.

Turner, R. M.., J. E. Bowers, and T. L. Burgess. 1995. Sonoran Desert Plants: an ecological atlas. University of Arizona Press, Tucson, AZ.

Vaughn, T. A. 1990. Ecology of living packrats. *In*, Packrat Middens: the last 40,000 years of biotic change, J. Betancourt, T. R. Van Devender, and P. S. Martin (eds.). The University of Arizona Press, Tucson, AZ.

Warren, P. L., K. L. Reichhardt, D. Mouat, B. T Brown, and R. R. Johnson. 1982. Technical Report No. 9, Vegetation of Grand Canyon National Park. Cooperative National Park Resources Studies Unit, University of Arizona. Tucson, AZ.

Whittaker, R. H. 1951. A criticism of the plant association and climatic climax concepts. Northwest Science 25: 17-31.

Whittaker, R. H. and Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: A gradient analysis of the south slope. Ecology, 46: 429-452.

Whittaker, R. H. and Niering. 1968B Vegetation of the Santa Catalina Mountains, Arizona, III. Species Distribution and floristic relations of the north slope. Journal of the Arizona Academy of Sciences, 5: 3-21.

Whittaker, R. H. and Niering. 1968A Vegetation of the Santa Catalina Mountains, Arizona, IV. Limestone and Acid Soils. Journal of Ecology, 56: 523-544.