INDIVIDUALISTIC AND PHYLOGENETIC PERSPECTIVES ON PLANT COMMUNITY PATTERNS

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ABSTRACT

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Individualistic and Phylogenetic Perspectives on Plant Community Patterns

(Under the direction of Robert K. Peet)

Plant communities have traditionally been viewed as spatially discrete units structured by dominant species, and methods for characterizing community patterns have reflected this perspective. In this dissertation, I adopt an an alternative, individualistic community characterization approach that does not assume discreteness or dominant species importance *a priori* (Chapter 2). This approach was used to characterize plant community patterns and their relationship with environmental variables at Zion National Park, Utah, providing details and insights that were missed or obscure in previous vegetation characterizations of the area.

I also examined community patterns at Zion National Park from a phylogenetic perspective (Chapter 3), under the assumption that species sharing common ancestry should be ecologically similar and hence be co-distributed in predictable ways. I predicted that related species would be aggregated into similar habitats because of phylogenetically-conserved niche affinities, yet segregated into different plots because of competitive interactions. However, I also suspected that these patterns would vary between different lineages and at different levels of the phylogenetic hierarchy (phylogenetic scales). I examined aggregation and segregation in relation to null models for each pair of species within genera and each sister pair of a genus-level vascular plant

supertree. Some pairs confirmed predictions, but many others did not, suggesting niche divergence rather than niche conservatism.

In the final chapter, I discuss community characterization from a phylogenetic perspective, exploring the possibility of using phylogenetic units in lieu of species in community analysis. I consider scenarios where species may not be optimal units of analysis, such as broad-scale community studies spanning species range limits. In such scenarios, species sharing common ancestry could potentially be merged and treated as a single unit. I present a method for identifying such species that I developed by adding a phylogenetic dimension to species clustering. This method is demonstrated through an analysis of bog and rock outcrop plant communities of the Southern Appalachian Mountains.

To my grandfather James. A. Ott,
scientific thinker and admirer of Southern Utah’s natural wonders

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CHAPTER 1

INTRODUCTION

This dissertation deals with plant communities: how they are conceptualized, sampled and characterized; and the environmental, evolutionary and historical factors influencing their composition and distribution. Describing and understanding plant communities is an important component of the discipline known as plant community ecology or vegetation science (Mueller-Dombois and Ellenberg 1974, Kent and Coker 1991). Building on this research tradition, I have sought to characterize and interpret plant community patterns for a specific area of interest: Zion National Park, Utah. I have also sought to contribute to the conceptual and methodological advancement of this field by synthesizing concepts, offering new perspectives and developing new approaches for community analysis.

The main chapters of this dissertation revolve around two themes, (1) the individualistic concept of the plant community and (2) phylogenetic community organization. The purpose of this introductory chapter is to briefly explain how these seemingly disparate concepts relate to one another in the context of community characterization.

Plant communities have traditionally been characterized and mapped as discrete units differentiated based on composition, structure or physiognomy. Floristic community classifications systems such as those developed by the Zurich-Montpelier school of phytosociology (Braun-Blanquet 1965, Ewald 2003) or the U.S. National Vegetation Classification (Jennings et al. 2009) use taxonomic composition, generally at the species level, as the primary criteria for differentiating community units. Plant communities are thus commonly portrayed as species assemblages occurring within discretely-defined spatial areas. From an individualistic perspective, this portrayal is problematic because species may not be co-distributed in a discrete manner, whereas from a phylogenetic perspective, the species emphasis conceals evolutionary relationships that may be relevant to community organization.

The individualistic concept as developed by Gleason (1926, 1939) addresses the variable nature of species distributions and environmental responses. Gleason pointed out that community boundaries may not be easily identified because of this individualistic variability. Subsequent authors influenced by Gleason's work developed alternatives to community classification (e.g., ordination) that do not require discrete community classes (Whittaker 1967, Mueller-Dombois and Ellenberg 1974, Kent and Coker 1992, McCune and Grace 2002). Others have used the individualistic concept to justify species-specific as opposed to community-level environmental modeling (e.g. Evans and Cushman 2009). The individualistic concept has been interpreted by some to mean that individual species distributions bear no relation to one another and that community units are entirely arbitrary constructs (Shipley and Keddy 1987, Leibold and Mikkelson 2002). However, Gleason's (1926, 1939) view was more balanced in that he acknowledged the existence of recurring community patterns, including species sharing sufficiently similar environmental responses to justify their recognition as ecological species groups. This balanced perspective between species individualism and similarity underlies the “individualistic species group” approach that I use to characterize plant community patterns of Zion National Park (Chapter 2). Instead of assuming that species are organized into discrete community units, I assume that some species are more similarly distributed along environmental gradients than others, and use cluster analysis to identify such species groups. Since species groups are spatially-diffuse constructs, this approach leads to continuous-scale representations of spatial community variability.

The notion that all species are distributed independently of each other can be countered on ecological and evolutionary grounds. Plant species interact, often through competition or other negative interactions that limit their ability to coexist (Silvertown 2004), but also through positive interactions such as facilitation that promote coexistence (Callaway 1997). Species attributes related to local coexistence comprise what has become known as the alpha niche, as contrasted with beta niche attributes related to species responses along environmental gradients (Pickett and Bazazz 1978, Silvertown et al. 2006). Alpha and beta niche attributes are likely to be similar in species sharing recent common ancestry because of phylogenetic niche conservatism, or the tendency for niche attributes to be retained over evolutionary time (Harvey and Pagel 1991, Webb et al. 2002). Species with conserved alpha niches might be expected to compete for resources and thus be segregated at local scales, while species with conserved beta niches might be expected to be aggregated with respect to environmental gradients (Webb et al. 2002, Silvertown et al. 2006, Cavender-Bares et al. 2009)—hypotheses that I examine for plants of Zion National Park in Chapter 3. Phylogenetic niche conservatism thus provides reason to expect non-random, non-individualistic distribution patterns among at least some species in communities.

Whereas proponents of the individualistic concept may prefer that species be treated as independent units in community studies, proponents of the phylogenetic perspective may argue that species are not statistically independent and should be examined only in a phylogenetic context (Harvey and Pagel 1991, Harvey et al. 1995). The phylogenetic perspective has fueled the recent development of metrics for measuring phylogenetic relatedness and phylogenetic diversity of communities (Webb 2000, Webb et al. 2002, Hardy and Senterre 2007, Helmus et al. 2007, Graham and Fine 2008, Cadotte et al. 2010). These metrics offer phylogenetic alternatives to the species-based metrics commonly used in community characterization and analysis (e.g., McCune and Grace 2002). In many respects, this emerging field of phylogenetic community analysis parallels the earlier emergence of continuum analyses such as ordination. Phylogeny transforms taxonomic units into continuous fields of relatedness, just as ordination transforms community units into continuous fields of compositional similarity. In both cases, continuous representations of community patterns may be useful but also carry certain drawbacks. For phylogenetic community analysis, a major drawback is that the presumed correlation between phylogenetic relatedness and niche similarity may not be consistent across lineages with different evolutionary histories (Giannini 2003, Losos 2008). In some lineages niche conservatism may be essentially overridden by rapid niche divergence, as in adaptive radiations (Levin 2005, Ackerly 2009). Even in lineages exhibiting niche conservatism, the degree of conservatism may differ for different niche attributes. Some types of niche conservatism may only be detectable or relevant at narrow phylogenetic scales (e.g. between closely-related species within a genus).

In light of these drawbacks of strictly continuous phylogenetic community analysis, I propose an alternative approach that incorporates phylogenetic information but recognizes discontinuities of phylogenetic niche conservatism. Instead of dissolving taxonomic units into measures of phylogenetic relatedness, I advocate an approach that maintains unit structure but merges units when niche conservatism is evident. Species are merged into broader phylogenetic units if they show similar habitat (beta niche) affinities, as inferred from their association patterns with other species (or other merged phylogenetic units). I implement this approach through an algorithm derived from the species clustering algorithm used to identify species groups in Chapter 2. The new algorithm (multilevel ordered coalition clustering) is presented in Chapter 4, along with an explanation of its conceptual basis and applicability. Reasoning that this approach may be most useful for community studies spanning large areas (with high spatial species turnover), I use plant community data drawn from the Southern Appalachian region to demonstrate the new algorithm.

Chapter 4, which caps this dissertation, also includes a discussion of parallels between spatial scale and phylogenetic scale in community studies. Following previous treatments of spatial scale (Levin 1992, Scheiner et al. 2000), I introduce grain, extent and focus as components of phylogenetic scale.

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CHAPTER 2

INDIVIDUALISTIC PLANT SPECIES GROUPS OF ZION NATIONAL PARK

ABSTRACT

Questions: Can plant community characterization be carried out in a manner consistent with Gleason's individualistic concept? What new insights can be obtained by redefining communities in terms of individualistic species groups rather than discrete vegetation units?

Location: Zion National Park, Utah, U.S.A.

Methods: Individualistic community characterization is demonstrated through re-analysis of a systematically-sampled vegetation dataset. Overlapping species groups identified through coalition clustering ('coalition groups') were treated as individualistic equivalents of faithful species, while 'affiliate' species having high co-occurrence and high cover with respect to these groups were treated as constant and dominant species, respectively. Environmental affinities of each coalition group were modeled and mapped through regression tree analysis. Results were compared with two previous vegetation characterizations of the park.

Results: Coalition groups overlapped spatially and compositionally, especially in terms of affiliate species, but each represented a unique pattern with interpretable environmental relationships. A mesic gradient from low-elevation riparian zones through mid-elevation narrow canyons to high-elevation environments was represented by three overlapping coalition groups. Two groups occupying slickrock and sand environments were detected on the Navajo Sandstone, as well as two on mesa tops above it. At lower elevations, three intergrading xeric coalition groups were distinguished. These patterns had been obscured in previous vegetation characterizations that had demanded discrete units, emphasized dominant species, applied a physiognomic classification hierarchy and/or sampled non-systematically.

Conclusions: The coalition clustering approach achieved community characterization objectives without assuming spatial discreteness or dominant species preeminence. The individualistic concept is not only compatible with community characterization, but provides a solid conceptual framework for interpreting community patterns.

INTRODUCTION

Gleason's (1926, 1939) individualistic concept, though widely recognized and accepted by contemporary plant ecologists, remains at the margins of plant community characterization activities. The individualistic concept emphasizes the unique distribution patterns and ecological requirements of individual species, and therefore questions the assumption that communities are discrete, integrated units (Gleason 1926, 1939). Gleason's criticisms of discrete community classification were initially dismissed, but influenced the later development of continuous community modeling approaches such as ordination (McIntosh 1975). The individualistic concept also eventually became more widely favored than Clements' (1916) organismal concept, which views communities as integrated entities structured by their dominant plant species (Clements 1916, 1936, McIntosh 1975, Eliot 2007). Despite these developments, discrete vegetation classification emphasizing structural dominants continues to be a popular approach for characterizing plant communities. The U.S. National Vegetation Classification System (NVCS), for example, seeks to define spatially discrete units that can be recognized by their dominant species, structure and physiognomy (Grossman et al. 1998, FGDC 2008, Jennings et al. 2009).

The continued practice of discrete vegetation classification has been justified on the grounds of convenience and utility. Discrete community models are relatively easy to describe and map because of their well-defined boundaries. Proponents of the NVCS acknowledge that community boundaries may not be as sharp as their models depict, but argue that they provide useful, if sometimes arbitrary, partitions of community variation (Grossman et al. 1998, Comer et al. 2003). Even Curtis (1959), widely regarded as a pioneer in ordination approaches, recognized the practical value of dividing continuous community variation into discrete units. Working with these units, Curtis (1959) was able to characterize community features such as prevalent species (commonly encountered within a community) and modal species (concentrated within a community), much as others have done elsewhere using the essentially equivalent terms *constant species* and *faithful species* (Barkman 1989, Kent and Coker 1992). Constancy and fidelity are useful concepts for conveying ecological information about individual species and allowing community units to be identified in the field. Species that are both constant and abundant (dominant species) are especially useful for visualizing and identifying community units, whether from the ground or from an aerial view. Signatures of community dominants in aerial or satellite imagery are now routinely used in vegetation mapping applications, including those related to the NVCS (e.g., Cogan et al. 2004, Faber-Langendoen et al. 2007). Ancillary environmental data are also often integrated with community data so that environmental factors responsible for community distributions can be inferred (Mueller-Dombois and Ellenberg 1974, Kent and Coker 1992, McCune and Grace 2002). In short, discrete vegetation classification is a well-established, practical means for condensing and presenting valuable ecological information.

Can the useful products of discrete vegetation classification—compositional, spatial and environmental representations of plant community patterns—be obtained without dismissing the individualistic concept? What are the benefits of aligning community classification practices more closely with individualistic principles? This paper addresses these questions by formulating and applying individualistic alternatives to conventional vegetation mapping, environmental modeling and compositional characterization (including faithful, constant and dominant species). Using novel extensions of existing techniques such as coalition clustering (Sanderson et al. 2006) and regression tree modeling (Breiman 1993), I demonstrate an ‘individualistic species group approach’ that characterizes communities without requiring discrete community units or over-emphasizing dominant species.

The ‘individualistic principles’ that guide this approach are found in the original writings of Gleason. Gleason stressed the fact that each plant species carries its own history and is to some degree ecologically unique:

> In conclusion, it may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements (Gleason 1926, p. 26).

By emphasizing individualistic variability in plant species distributions due to different migration histories and environmental affinities, Gleason countered the notion that plant associations (community units) are sufficiently distinct, discrete and integrated to be unambiguously classified on the basis of species composition or vegetation structure. He did not, however, deny that recurring patterns approximating discrete communities can often be observed in nature (Gleason 1926, p. 25-26). Gleason recognized that species individualism (spatial and ecological uniqueness) is itself a matter of degree, with some species demonstrating a greater degree of similarity than others:

> The [individualistic] concept is by no means opposed to the recognition of the synusia, or union, defining it as a group of plants whose physiological demands are so similar that they are regularly selected by the same environment and consequently regularly live together (Gleason 1939, p. 108).

Hence an individualistic approach to community characterization permits the dual objective of identifying ecologically similar species, while also recognizing and quantifying their differences.

The “unions” mentioned by Gleason later came to be referred to as “ecological species groups” by plant ecologists in Europe and elsewhere (Mueller-Dombois and Ellenberg 1974, Abella and Shelburne 2004). Analogous “sociological species groups” defined by overlapping distribution patterns were promoted by Doing (1969). Relaxing the requirement that species within a group belong to the same life form leads to the definition of “species group” often used in contemporary community studies: a set of species with similar distributions among community samples, typically identified through cluster analysis (Austin and Belbin 1982, Ferrier et al. 2002, McCune and Grace 2002). The “individualistic species groups" presented in this paper have the additional distinction of being quasi-independent, potentially-overlapping species sets. They also serve as substitutes for faithful species and provide starting points for community characterizations that are spatially continuous and not biased toward dominant species.

The individualistic species group approach is demonstrated for plant communities of Zion National Park (Zion), an important conservation area in Utah, U.S.A. with pronounced topographic, edaphic, and hydrological variation. Relatively abrupt transitions between geologic substrates, xeric and mesic zones, exposed and shaded slopes, and lower and upper elevations are noticeable in some areas of Zion, but in other areas these environmental gradients are more subtle and gradual (Biek et al. 2003, Sharrow 2007a, 2007b). Zion houses a rich flora including over 900 native species that are differentiated among the park's environments (Fertig and Alexander 2009), yet relatively few plant species are dominants (Harper 1993, Harper et al. 2001, Cogan et al. 2004, Fertig and Alexander 2009). These characteristics of Zion suggest that an examination of community patterns without bias toward discrete zonation or dominant species would be an appropriate compliment to previous studies.

Specifically, this paper presents a re-analysis of the dataset that Harper (1993) and Harper et al. (2001) used to characterize the vegetation of Zion. In the previous analysis, vegetation survey plots were classified into vegetation types whose constant and faithful species were described using Curtis' (1959) prevalent and modal species concepts (Harper 1993, Harper et al. 2001). In the current analysis, faithful species take the form of individualistic species groups derived directly from association patterns through cluster analysis, and constant species are defined as species that tend to co-occur with these species groups. Ten individualistic species groups are presented along with their co-occurring species, environmental relationships and distribution. These results are compared with the previous vegetation characterizations of Harper et al. (2001) as well as those of Cogan et al. (2004) who applied the NVCS at Zion.

BACKGROUND

Study Area

Zion National Park (Zion), Utah, U.S.A. was established in 1919 to protect the striking scenery of Zion Canyon, where massive walls of the Navajo Sandstone formation tower above the Virgin River (NPS 2009). Subsequent expansion to include surrounding canyons, mesas and lowlands brought the park to its current ca. 590 km^2 (Cogan et al. 2004, NPS 2009). Zion is comprised of two roughly rectangular sections (Fig. 2.1), a large southeastern section that includes Zion Canyon and Coalpits Wash (lowest elevation in Zion, 1128 m) and a smaller northwestern section that includes the Kolob Canyons and Horse Pasture Plateau (highest elevation in Zion, 2660 m) (Cogan et al. 2004).

Zion lies at the western edge of the Colorado Plateau physiographic province, bordering the Basin and Range province to the west at the Hurricane fault escarpment (Biek et al. 2003). The Basin and Range can be further divided into the higher-elevation Great Basin northwest of Zion and the lower-elevation Mojave Desert to the southwest. The Colorado Plateau, Great Basin and Mojave Desert have been recognized as distinct floristic regions (McLaughlin 1986, 1989); and Zion, because of its position near their intersection, contains floristic elements characteristic of each (Meyer 1978, Cogan et al. 2004, Fertig and Alexander 2009).

Zion has a semiarid climate with seasonal temperature changes and precipitation concentrated in winter/spring frontal storms and late-summer monsoons (Woodbury 1933, Mortensen et al. 1977, Sharrow 2007b). During the period 1959-1989 (i.e., 30 years preceding the 1987-89 vegetation survey discussed below), mean annual precipitation at the Zion Canyon weather station (1234 m) was 388 mm and mean annual temperatures were 6.3^{o} C in January and 34.5^{o} C in July (UCC 2010). Local climate varies along the 1128-2660 m elevation gradient (Cogan et al. 2004) and is further modified by topographic position and exposure. Moisture is concentrated in seeps and springs that emerge from porous substrates, and in permanent and intermittent streams that are periodically exposed to flash flood disturbance (Sharrow 2007a).

Horizontally-aligned exposures of sedimentary rocks, including both cliff and bench-forming strata, are prominent at Zion. The oldest (Permian to Early Jurassic) strata occur at low elevations on the southwestern side of the park and on slightly higher elevations on the northwestern side where the Taylor Creek thrust fault disrupts their stratigraphic continuity (Biek et al. 2003, O'Meara 2006). These strata, which include the Kiabab, Moenkopi, Chinle, Moenhave and Kayenta formations, contain alternating bands of mudstone, siltstone, sandstone, conglomerate, limestone and gypsum (Biek et al. 2003). The badlands, slopes, and small cliffs of these lower formations at Zion are dwarfed by the massive cliffs and 'slickrock' exposures of the overlying Jurassic Navajo Sandstone (Biek et al. 2003). The stratigraphic sequence is topped by Middle Jurassic and Cretaceous sandstone, limestone, shale and gypsum deposits of the Temple Cap, Carmel and Cedar Mountain formations (Biek et al. 2003, O'Meara 2006). The entire sequence is in turn partially overlain by Quaternary deposits including volcanic basalt flows and cinder cones, alluvium, lacustrine, landslide, talus, residual and eolian deposits (Biek et al. 2003, O'Meara 2006, Sharrow 2007a).

Soil development has been inhibited in many areas of Zion because of rapid erosion by water, wind and gravity, leading to exposed rock outcrops in some areas and recent deposits with limited soil profile development (entisols) in others (Mortensen et al. 1977, Biek et al. 2003, Sharrow 2007a). Aridisols and mollisols are also present in Zion at lower and higher elevations, respectively; and alfisols can be found at the highest elevations (above 1830 m) (Mortensen et al. 1977).

Many of Zion’s geologic substrates and their derivative soils have distinctive physical and chemical properties that pose challenges to plants, as exemplified by the bentonite shrink-swell clays of the Petrified Forest member of the Chinle Formation and the solid slickrock surfaces of the Navajo Sandstone (Biek et al. 2003, Sharrow 2007a, Cogan et al. 2004). In other instances substrate and hydrology combine to favor plant growth, as in the hanging gardens that occur on seepage areas of canyon walls (Malanson and Kay 1980, Welsh 1989).

Substrate variation and gradients of moisture and temperature related to hydrology, topographic position, exposure and elevation have produced a variety of different vegetation types at Zion (Woodbury 1933, Harper 1993, Harper et al. 1992, 2001, 2003, Cogan et al. 2004). As a general pattern, desert shrublands and grasslands at lower elevation, more exposed sites give way to coniferous woodlands, mountain brush, and montane forests and grasslands at higher elevation, less exposed sites (Harper 1993, Cogan et al. 2004). Riparian areas and wetlands, which are most extensive at lower elevations, are occupied by various forest, woodland, shrubland and herbaceous vegetation types (Harper et al. 1992, Cogan et al. 2004).

Although most of Zion currently has an undeveloped wilderness character, the park is not free of human disturbance. Euro-American settlement beginning in the mid-1800s led to agricultural clearing in low-elevation floodplains and widespread livestock introductions throughout the Zion area (Woodbury 1933, Madany and West 1983). Heavy livestock grazing in the early part of the twentieth century followed by fire suppression later in the century favored an increase of woody plants at the expense of grasses and forbs (Madany and West 1983, Jeffries and Klopatek 1987). Isolated mesas in the central portion of the park escaped grazing impacts because of their inaccessibility (Madany and West 1983, 1984). More recently, livestock have been removed but mule deer (*Odocoileus hemionus*) have increased in areas of high human visitation, resulting in declines in cottonwood (*Populus fremontii*) and other riparian species (Ripple and Beschta 2006). The vegetation survey data used here record a snapshot of conditions following 30+ years of livestock exclusion. The troublesome invasive species cheatgrass (*Bromus tectorum*), red brome (*B. rubens*), ripgut brome (*B. diandrus*) and tamarisk (*Tamarix* spp.) were already well-established in Zion at the time of sampling.

BYU-RMRS Vegetation Characterization (Harper et al. 2001)

The first park-wide, plot-based vegetation survey of Zion was carried out in 1987-1989 by workers affiliated with Brigham Young University (BYU) and the Rocky Mountain Research Station (RMRS, formerly the Intermountain Research Station) Shrub Sciences Laboratory of the U.S. Forest Service. This survey, which I refer to by the acronym BYU-RMRS, is the primary source of species occurrence data for the current study. The survey has previously been described in a series of reports and manuscripts (Harper 1993, Harper et al. 1992, 2001, 2003). Data from the BYU-RMRS survey will soon be archived in the VegBank repository (ESA 2010).

The BYU-RMRS survey implemented a systematic sampling strategy in which U.S. Geological Survey (USGS) cadastral section corners and corresponding park boundary markers served as sampling targets (Fig. 2.1-2.2). In addition to 270 plots located at or near these markers, 18 plots were placed using subjective criteria in order to capture spatially-restricted plant communities (riparian areas, hanging gardens, and old fields). The standard plot was a 100 m^2 circle with the exception of six equivalently-sized plots that were rectangular or square. Data collected within plots included vascular plant species composition following Welsh et al. (1987), cover classes for each species according to the Braun-Blanquet system (Braun-Blanquet 1965), and percent cover of bare soil, rock, litter and cryptogams (Harper 1993, Harper et al. 2001).

Harper (1993) used the BYU-RMRS survey data to classify the vegetation of Zion into ten discrete vegetation types that were concisely summarized in a subsequent manuscript (Harper et al. 2001). The vegetation types were recognized on account of being “commonly used by land managers in the area” (Harper et al. 2001) and each plot was intuitively assigned to a vegetation type based on dominant species and environmental context. Plot data were then used to characterize attributes of each vegetation type including prevalent and modal species following Curtis (1959). Prevalent species are defined as the most frequently encountered species (occurring in the most plots) within a community or vegetation type, where the number of prevalent species is equal to the species density (average number of species per plot) for the community (Curtis 1959, Harper et al. 2001). Modal species are defined as prevalent species that reach their greatest frequency in a given community relative to other communities under study. In Harper et al. (2001), modal species were identified for each vegetation type relative to the others described at Zion.

The Hanging Gardens vegetation type described by Harper et al. (2001) incorporated additional data from published studies to supplement the hanging garden plots captured by the BYU-RMRS survey. Twenty-one hanging gardens described by Malanson and Kay (1980) and Welsh (1989) were treated as plots for characterizing this vegetation type (Harper 1993, Harper et al. 2001). These hanging garden data were excluded from the current analysis, which used only the 288 standard-sized plots of the BYU-RMRS survey.

USGS-NPS Vegetation Characterization and Mapping (Cogan et al. 2004)

Another round of extensive vegetation sampling at Zion took place in 1999-2000 through a partnership of the USGS, U.S. National Park Service (NPS), U.S. Bureau of Reclamation and NatureServe (Cogan et al. 2004). New vegetation plot data were deemed necessary to meet the standards of the USGS-NPS Vegetation Mapping Program which aims to apply the U.S. National Vegetation Classification System (NVCS) to all U.S. National Park units (USGS 2010). Zion was among the first parks to be targeted by this program because the program's products were in demand by park managers (Cogan et al. 2004). The plot data, vegetation descriptions, GIS layers and other products from this program (USGS 2004) proved useful in the current study for comparative and interpretive purposes.

The USGS-NPS vegetation survey sampled 346 circular, square or rectangular plots (Fig. 2.2) ranging from 100 m^2 to 400 m^2 where plant species were identified following Kartesz (1999) (USGS 2004, Cogan et al. 2004). A gradsect strategy (Gillison and Brewer 1985) was used to divide Zion into biophysical units (BPUs) that were mapped and targeted for field sampling. Each of the 70 BPUs mapped at Zion was defined by a unique combination of categorical environmental variables (two hydrology, two fire history, four solar insolation and nine geology/elevation categories) developed as GIS layers specifically for this purpose (Cogan et al. 2004). Accessible polygons of each BPU were targeted by field survey teams who ultimately placed plots on sites deemed representative of major vegetation types and relatively homogeneous in terms of vegetation structure and composition (Cogan et al. 2004). GPS coordinates were recorded for each plot.

Cogan et al. (2004) used the USGS-NPS plots to classify and map the vegetation of Zion following the NVCS. Multivariate analysis of species data, including cover class by strata recorded for each species, helped guide the classification process (Cogan et al. 2004). Each plot was assigned to an association (the standard lowest level of the NVCS hierarchy) nested within an alliance and other higher hierarchical levels (formation, subgroup, group, subclass, and class). Association descriptions (Cogan et al. 2004, Appendix F) include references to “characteristic species” and “associated species” that can be interpreted as constant and/or faithful species, although the basis for their derivation is not explicitly explained.

In conjunction with plot sampling and classification, aerial photo interpretation techniques were used to map vegetation types across the entire park, guided by the areal orthophoto signatures associated with each plot (Cogan et al. 2004). Mappers sought to follow the NVCS with as much resolution as possible but not all vegetation was discernable or separable at the association level. The final vegetation map, published in digital format, contains 76 map units: 23 associations (including one association separated into two phases), six alliances, two mosiacs (associations too intermixed to separate), 16 complexes (associations too similar to distinguish), and 29 miscellaneous units (unclassified vegetation and non-vegetated areas) (Cogan et al. 2004). This discrete vegetation map provided a framework for comparison with the individualistic species group environmental affinity maps of the current study.

INDIVIDUALISTIC COMMUNITY CHARACTERIZATION: CONCEPTS AND METHODS

Conceptual Overview

The objective of the present analysis is to re-characterize plant communities at Zion National Park through an individualistic approach based on spatially-diffuse species groups rather than discrete vegetation units. I begin my description of this approach with a brief conceptual summary.

Species groups, defined broadly as species belonging to multiple life forms with overlapping distributions across community samples, are conceptually similar to faithful species. Members of a species group are ‘faithful’ to each other across an entire study area, but not necessarily faithful to discretely-defined communities within the area. This conceptual parallel provides the rationale for substituting faithful species with species groups in the individualistic approach presented here. The approach exchanges the need for identifying discrete community units with the need for discrete species groups, but also acknowledges individualistic variation of species by quantifying their affinity (degree of association) relative to a group. *Affinity* to a species group replaces *fidelity* to a community unit in the individualistic species group approach. Furthermore, the approach allows species to belong to and/or have high affinities to more than one species group, which differs somewhat from conventional thinking about community fidelity but is compatible with the individualistic concept.

The individualistic species group approach also incorporates a conceptual equivalent of constant species. Whereas *constancy* is normally quantified as the frequency of *occurrence* of a species within a *community unit*, the analogous *affiliation* value presented here is the frequency of *co-occurrence* of a species with members of a *species group*. Constancy is an inherently individualistic measure, in the sense that it is calculated for each community unit independently and hence a species can be constant in multiple communities. In the same way, species can be independently affiliated with multiple species groups in the approach followed here.

An important feature of the individualistic species group approach is that it allows spatial community variation to be represented as continuous fields of species group affinity. Because species groups are spatially-diffuse patterns of multiple species across multiple sites, individual sites (e.g. community sample units) generally do not correspond exactly to any given species group. A given site may house many members a given species group, or few members, or a mixture of species with different degrees of affinity to the group. Such differences can be quantified by averaging the affinity values of the species present at a site (essentially a form of weighted averaging; Kent and Coker 1992, McCune and Grace 2002). Community sample units can thus be placed along a continuum of affinity values for each species group, congruent with Gleason’s (1926, 1939) individualistic concept in relation to sites. This approach opens the door for quantitative spatial and environmental analyses of species group affinities. In the application presented here, relationships between site-averaged species group affinities and environmental variables are modeled using regression tree analysis (Breiman 1993). This leads to descriptions of *environmental affinities* of species groups, in which the term *affinity* again carries a specific quantitative meaning, in this case denoting the environmental conditions of sites where species group affinity is comparatively high.

A final point is that individualistic species groups can be compared with discrete community units wherever both have been characterized for the same study area. One way of quantifying the correspondence between a species group and a community unit is by averaging the group affinity values of species attributed to the unit (an extension of the weighted averaging technique described above). Affinity can be averaged for all species occurring in plots belonging to the unit, or more specifically for the unit's faithful species. Spatial models of species groups and community units can also be compared. A combination of these procedures was used in the comparisons presented here.

Coalition Clustering and Affinity Calculations (Individualistic Fidelity Analysis)

Coalition clustering, a non-hierarchical agglomerative clustering algorithm included in the program RCLUS (Sanderson et al. 2006) provided a means for identifying the individualistic equivalent of faithful species at Zion without having to define community units. RCLUS was developed as a tool for R-mode (species-based) clustering of community datasets. The name *coalition clustering* underscores the individualistic variability of species within the clusters ('coalitions') that the algorithm builds. Coalition clustering generates clusters of positively associated species here referred to as *coalition* *species groups* or simply *coalition groups*. The term *core species*, used by Sanderson et al. (2006) to refer to species belonging to a group, is here replaced by the term *coalition species*.

Different coalition clustering solutions can be obtained by varying three user-defined parameters of the algorithm: association coefficient, threshold association value, and minimum number of occurrences for species inclusion in groups (see below). In addition, clustering solutions may vary from one run of the algorithm to another because of the random nature of the agglomerative process. The clustering solution presented here was selected from among a small number of variants obtained using the phi coefficient at a threshold value of 0.15, and allowing species occurring in at least three plots to be included in groups. These parameter values yielded eleven coalition groups, providing a numerically-congruent alternative to the ten vegetation types previously described for Zion by Harper et al. (2001). Dr. S.C. Sanderson, author of the RCLUS program and former field crew leader for the BYU-RMRS survey, played a key role in analyzing and selecting this clustering solution.

Coalition Clustering in RCLUS begins with a matrix of association between species pairs. Association coefficients measure the degree to which two species show the same pattern of presence and absence in a dataset, calculated from the cells of a two-way presence-absence contingency table:

		Species 1	
		Present	*Absent*
Species 2	*Present*	*a*	*b*
	Absent	*c*	*d*

The phi coefficient incorporates all four cells of the table according to the formula:

$$\text{phi coefficient} = \frac{ad - bc}{\sqrt{(a+b)(a+c)(b+d)(c+d)}}$$

Phi ranges from -1 (negative association) to +1 (positive association) and is independent of the total number of occurrences in the table (Jackson et al. 1989, Tichý and Chytrý 2006). This is a useful property for measuring association, but makes the phi coefficient ineffective at measuring statistical significance (unlike the related chi-square). If one or both species has low occurrence in the dataset, the statistical significance of the association may be in question, but association is still quantifiable. The RCLUS user's option of excluding species of low frequency from cluster analysis is important for this reason.

Clustering proceeds by agglomerating species whose mean association is higher than the user-defined threshold value. That is, when pairwise association values are averaged for all species pairs in a group, the average must exceed the threshold for the group to be accepted. The algorithm initiates the first group with a randomly-selected species and then randomly cycles through the remaining species, adding them to existing groups or initiating new groups as appropriate. Coalition Clustering allows species to belong to multiple groups with the exception that species already present in an existing group cannot initiate a new group. The algorithm undergoes several cycles of adding and removing species allowing the composition of species groups to stabilize. By defining a critical threshold for mean association within groups, the user determines how loose or tight the groups are allowed to be. High thresholds tend to produce many small groups in contrast to few large groups at low thresholds (Sanderson et al. 2006).

Once the Coalition Clustering algorithm is complete, RCLUS saves the mean association value of each species to each group (Sanderson et al. 2006). These mean association values, or *affinity values*, provide a quantitative measure of the relationship between individual species and coalition groups.

Affiliation Calculations (Individualistic Constancy and Dominance Analysis)

RCLUS also contains a function that calculates *percent co-occurrence* (previously named *mean percent*) of each species to each coalition group. Percent co-occurrence is calculated by summing joint presences across all pairings of a focal species with the species comprising a coalition group and then standardizing by the maximum possible number of joint presences. Using the notation of presence-absence frequencies, this can be represented as follows:

		Focal Species	
		Present	*Absent*
Coalition Species	*Present*	*a*	*b*

$$\text{percent co-occurrence} = \frac{\sum_{sp1}^{spN} a}{\sum_{sp1}^{spN} (a+b)}$$

Restated using this notation, percent co-occurrence of the focal species to the coalition group is the sum of joint presences between the focal species and each of the coalition species in the group (*sp1* to *spN*), standardized by the total number of occurrences of all the coalition species.

The intuitive term *affiliation* is here used interchangeably with percent co-occurrence. Species belonging to a group are naturally likely to have high affiliation with their own group. However, correspondence between high group affinity and high affiliation need not be exact because the former measures specificity (fidelity) while the latter measures commonness (constancy). A widespread generalist species can be highly affiliated with multiple groups without demonstrating high affinity for any of them.

Building on Sanderson's RCLUS analysis of the BYU-RMRS dataset, I added a step to extract a set of highly affiliated species ('affiliate species') for each coalition group. Since Curtis (1959) used species density, the mean number of species per plot in a community, to determine how many species to include in prevalent species lists, I followed an analogous procedure for determining the number of affiliate species for each coalition group. The species density of a coalition group was calculated as the mean number of species occurring in plots where coalition species occurred, weighting plots by how many coalition species they contained. Defining *S* as the species density of a coalition group, affiliate species are the *S* species with highest affiliation to the group.

Extending the affiliation concept further to include abundance as well as occurrence, I calculated the abundance of each affiliate species as its mean cover across plots containing coalition species, weighted once again by the number of coalition species per plot. Arithmetic midpoints of cover classes were used in these calculations. In this way I was able to identify the dominant species associated with each coalition group.

Environmental Modeling of Coalition Species Group Affinities

For each plot used in coalition clustering, RCLUS calculates the plot's affinity to each coalition species group as the average affinity value of the species recorded in the plot. Both coalition and non-coalition species contribute to these averages. I took these plot-averaged affinity values and used them to model correlative relationships between coalition groups and five environmental variables: elevation, slope, topographic exposure, topographic position, and geologic substrate (Fig. 2.3-2.4). These variables were selected because of they are easily-measured proxies for the major physical and chemical gradients affecting plant distributions at Zion. They were available or easily created as geographic information system (GIS) layers that were integrated with plot data in ArcGIS (ESRI 2003, 2004). My use of GIS-based environmental variables permitted predictive mapping of species group affinities beyond plot locations (Ferrier et al. 2006).

I manually digitized plot coordinates from the BYU-RMRS survey, originally marked on paper maps, with assistance from the primary field crew leader from the survey (S.C. Sanderson) using as references a high-resolution aerial orthophoto of Zion National Park (Cogan et al. 2004), digital USGS topographic maps and cadastral survey marker coordinates acquired through the USDI Bureau of Land Management (BLM 2006). Hawth's Tools, an ArcGIS add-in program (Beyer 2004), was then used to extract environmental data values for each plot based on its coordinates.

Two GIS layers served as sources of environmental data: a 10 m resolution digital elevation model (DEM) and a 1:24,000 scale digital geologic map built from multiple maps of Utah Geologic Survey (O'Meara 2006). These digital layers and accompanying metadata are now archived in the NPS data store (NPS 2010). They provide full coverage of Zion with the exception of the geologic map layer which omits ca. 1.3 km^2 along the western inner corner of the park. Although seven plots of the BYU-RMRS survey lie outside this layer, geologic units were easily assigned to these plots through visual interpolation from the edge of the geologic layer and examination of plot descriptions. These plots could thus be used in environmental modeling although the area missed by the geologic layer was ultimately excluded from predictive maps. The geologic layer was converted to raster format at the same resolution as the DEM prior to modeling and mapping.

Elevation was taken directly from the DEM, while slope and exposure were calculated using the *slope* and *hillshade* functions, respectively, in ArcGIS 9.0 Spatial Analyst (ESRI 2004). *Hillshade* was implemented at 215^{o} azimuth and 45^{o} altitude such that exposure values were highest on steep southwest-facing slopes where solar heat loading is expected to be highest (cf. McCune and Keon 2002). Topographic position was defined using the Topographic Position Index (TPI) developed by Weiss (2001). TPI was calculated for each pixel of the DEM by subtracting the mean elevation of surrounding pixels (within a defined radius) from the focal pixel's elevation (Weiss 2001, Jenness 2006). Negative TPI values indicate topographic lows such as canyon bottoms and positive values indicate topographic highs such as peaks and ridges. The ArcGIS 9.0 raster calculator (ESRI 2004) was used to calculate TPI at 50 m and 100 m radius.

A categorical variable map comprised of 16 geologic substrate classes (Fig. 2.4) was created through aggregation of the ca. 100 map units occurring within Zion according to O'Meara (2006). Most of the map units of O'Meara (2006) are individual members of geologic formations or descriptive categories for local Quaternary deposits. Given the need to simplify this map for modeling purposes, but acknowledging the many possible ways of merging map units, I settled on a pragmatic approach using lithology, spatial continuity and/or topographic characteristic as grouping criteria (Table 2.1, Fig. 2.4). Exploratory analyses (boxplots of coalition group affinities by substrate type) revealed that the eight major geologic formations of the park (Moenkopi, Chinle, Moenhave, Kayenta, Navajo, Temple Cap, and Carmel), though internally heterogeneous to various degrees, were likely to be useful categories for modeling community-environment relationships at Zion. Thus each formation was assigned its own class, except for poorly-represented ones at the lower end of the stratigraphic sequence (Kiabab) and upper end (Cedar Mountain) that were merged with the adjacent Moenkopi and Carmel formations, respectively. Exploratory analyses also supported a scheme in which Quaternary deposits were grouped according to their dominant depositional material (alluvium, colluvium, eolian, lacustrine, mass movement, residuum, and volcanics). The well-represented mass movement deposits were further split into three classes that occupy different topographic settings in the park: (1) talus, (2) slides/slumps/flows and (3) mixed (mass movement/colluvium/ alluvial pediment mantle) deposits (Table 2.1, Fig. 2.4). Map units of O'Meara (2006) included in each of these classes are shown in Table 2.1; note that some map units were not actually sampled by plots of the BYU-RMRS dataset but were assigned to the closest logical class.

Relationships between species group affinities and environmental variables were modeled using regression tree analysis (the `tree` function) in SPLUS 7.0 (Insightful Corp. 2005). Regression tree analysis generates a dichotomous tree model by splitting a dataset into progressively smaller subsets (Breiman 1993, Crawley 2007). Each split, represented by a node in the tree, segregates data points based on an ordinal relationship between a response variable and a predictor variable. The tree algorithm automatically selects the predictor variable with the strongest relationship at a given node if multiple predictor variables are supplied. Plot-averaged group affinity (in units of the phi coefficient) was the response variable and substrate class, elevation, slope, exposure, and topographic position (TPI at radius=50 m and radius=100 m) were the predictor variables used to build regression tree models for each coalition group. Models were built using consistent splitting rules (mincut=5, minsize=10, mindev=0.1). Multiple runs of random 10-fold cross-validation (the `cv.tree` function) were applied to each model to determine the best number of terminal nodes minimizing total deviance (Crawley 2007), and models were pruned accordingly.

Quantifying Correspondence with Previously-described Vegetation Units

In order to assess the correspondence between coalition groups identified through RCLUS analysis and vegetation types reported by Harper et al. (2001), results from both analyses were merged into a common database. Modal species listed for each vegetation type in Harper et al. (2001) were joined to their group affinity values from the RCLUS output, then averaged for each vegetation type/coalition group comparison. Two modal species (*Carex curatorum* and *Lobelia cardinalis*) were restricted to the supplemental hanging garden dataset used only by Harper et al. (2001) and were thus omitted from these calculations. All other species could be matched because of their common data source (the BYU-RMRS dataset).

I was also interested in quantifying the correspondence between coalition groups and NVCS associations reported by Cogan et al. (2004). Because modal species (or other types of faithful species) were not reported for these associations, I based my analysis on species composition of the raw plot data. That is, species recorded in plots of the USGS-NPS dataset were joined to coalition group affinity values, which were then averaged across all species occurrences for each association. This yielded association-averaged affinity values similar to the plot-averaged affinity values described previously (see "Environmental Modeling of Coalition Species Group Affinities"). As part of this process, taxonomic concepts in the USGS-NPS dataset were standardized to match Welsh et al. (2003). Following taxonomic standardization, 185 taxon records (including 71 taxa identified only to the genus level) remained unmatched because they were unique to the USGS-NPS dataset (Appendix 2.1); and conversely, 237 taxa captured by the BYU-RMRS survey were not represented in the USGS-NPS dataset (Appendix 2.2).

Mean coalition group affinities were also calculated for each mapped vegetation unit of Cogan et al. (2004). Using the zonal statistics tool in ArcGIS, pixel values from each species group affinity map were averaged for each vegetation unit.

RESULTS

Coalition Species Groups and Their Environmental Affinities

Eleven coalition species groups were identified through coalition clustering at a threshold value of phi=0.15. The eleven groups contain a total of 174 species extracted from the 511 species recorded by the BYU-RMRS vegetation survey (Appendix 2.2; updated to nomenclature of Welsh et al. 2003). One group containing six species (*Artemisia dracunculus*, *Elymus spicatus, Sisymbrium altissimum, Galium aparine*, *Physalis hederifolia*, and *Tragopogon dubius*) was excluded from further analysis because of its limited distribution in disturbed low-elevation environments. The remaining ten groups containing 9-36 species each (Table 2.2) can be readily described in terms of their environmental affinities at Zion (Fig. 2.5-2.14). I have given each species group a name that describes the environmental setting for which it demonstrates greatest affinity. Coalition species of each group are presented in descending order of affinity in Table 2.2 (left column) and an expanded table showing affinities of all species to all coalition groups is provided in Appendix 2.2. Coalition clustering's allowance for overlapping group membership resulted in 34 cases of species belonging to two groups and one case of a species (*Amelanchier utahensis*) belonging to three. Environmental affinities of coalition groups also overlap to varying degrees, as depicted in the predictive maps accompanying regression tree models in Figures 2.5-2.14. In the group descriptions that follow I highlight these cases of compositional and spatial overlap and interpret their ecological significance.

The Streambank group (Table 2.2A) contains several species, including *Baccharis emoryi*, *Salix exigua*, *Tamarix chinensis* and *Populus fremontii*, with clear affinities to low-elevation riparian zones at Zion. Regression tree analysis confirmed this inference by identifying low topographic positions [TPI (50 m radius) < -0.51] below 1356 m on alluvium or lacustrine substrates as the environmental conditions of highest affinity (Fig. 2.5). On substrates beyond alluvium and lacustrine, topographic lows continued to show higher affinities, but high elevations (>2321 m) also had relatively high affinities, presumably because mesic conditions at Zion's highest elevations are favorable for some riparian species. Indeed, the High Plateau group, which has highest affinity at elevations above 2243 m (Fig. 2.6), shares three coalition species (*Bromus carinatus*, *Elymus trachycaulus* and *Poa pratensis*) with Streambank (Table 2.2A-B). Coalition species unique to the High Plateau group include *Stellaria jamesiana*, *Lupinus sericeus*, *Prunus virginiana*, *Stipa lettermanii*, *Rosa woodsii*, and *Juniperus scopulorum*. (Table 2.2B).

The Crevice Canyon group (Table 2.2C, Fig. 2.7) occupies an environmental setting intermediate between Streambank and High Plateau, namely the bottom of narrow, mid-elevation Navajo Sandstone canyons where topographic shading and intermittent water flow produce cool mesic conditions. Sites with these conditions have extremely low TPI values; TPI (50 m radius) is less than -35 in the zone where Crevice Canyon affinities are highest (Fig. 2.7). Outside of these extreme topographic lows, the Crevice Canyon group has higher affinity for higher elevations (Fig. 2.7). This affinity pattern is mirrored by High Plateau's inverse pattern of high affinity for high elevations, intermediate affinity for narrow mid-elevation canyons (Fig. 2.6). The canopy dominant species *Abies concolor* as well as two herbs (*Thalictrum fendleri* and *Taraxacum officinale*) are coalition species of both Crevice Canyon and High Plateau (Table 2.2B-C). In addition, the Crevice Canyon group shares four species (*Acer negundo*, *Elymus canadensis*, *Equisetum hymenale* and *Agrostis exarata*) with the Streambank group (Table 2.2A) and five (*Heuchera rubescens*, *Zauschneria latifolia*, *Holodiscus dumosus*, *Selaginella underwoodii*, *Brickellia grandiflora*, and *Erigeron sionis*) with Slickrock (Table 2.2D). Crevice Canyon with 36 species is the largest of the coalition groups and many of its species were relatively uncommon with only 3-6 occurrences in the BYU-RMRS dataset (e.g., *Viola canadensis*, *Cystopteris fragilis*, *Polypodium hesperium*, *Galium triflorum*, *Rubus leucodermis*, *Mimulus guttatus*, *Disporum trachycarpum*) while others were more common with 10-29 occurrences (e.g. *Eupatorium herbaceum*, *Acer grandidentatum*, *Bromus ciliatus*, *Pseudotsuga menziesii*, *Philadelphus microphyllus*) (Table 2.2C).

Species associated with exposed Navajo Sandstone outcrops are represented in the Slickrock group which includes *Petrophytum caespitosum*, *Cercocarpus intricatus*, *Castilleja scabrida*, *Muhlenbergia thurberi* and *Ivesia sabulosa* (Table 2.2D). The Slickrock group had highest affinity on the Navajo Sandstone, especially above 1782 m, and had intermediate affinity on Carmel, Temple Cap, colluvium, residuum, and talus substrates (Fig. 2.8). Regression tree analysis further split the latter set of substrates based on topographic position revealing higher affinity at topographic lows [TPI (100 m radius) < -21] (Fig. 2.8). These topographic lows correspond to talus deposits immediately below Navajo Sandstone cliffs where sandstone substrate characteristics are to be expected. The Temple Cap formation immediately above the Navajo Sandstone is also primarily sandstone and would be expected to have similar plant species because of both substrate similarity and elevational proximity. On the other hand, the Slickrock group did not have high affinity for eolian deposits despite elevational proximity and common parent material.

Eolian deposits at Zion are composed primarily of sand and are especially extensive on the southeastern side of the park (O'Meara 2006, Fig. 2.4). Smaller pockets of sand associated with hollows and flat areas on Navajo Sandstone outcrops are scattered throughout the park. Many of these sand pockets were too small to be included on Utah Geologic Survey maps (i.e. O'Meara 2006) but were captured by plots of the BYU-RMRS survey. These plots contributed to the Upland Sands coalition group, which is characterized by sand-loving species such as *Cryptantha cinerea*, *Abronia fragrans*, *Artemisia campestris*, *Penstemon laevis*, and *Tradescantia occidentalis* (Table 2.2E). The shrub dominant *Arctostaphylos patula* is a coalition species of the Upland Sands group, while the tree dominant *Pinus ponderosa* is a coalition species of both Upland Sands and Slickrock, along with *Arenaria fendleri*, *Chrysopsis villosa* and *Linanthastrum nuttallii* (Table 2.2D-E). The regression tree model for the Upland Sands group (Fig. 2.9) is similar to the Slickrock model (Fig. 2.8), identifying higher-elevation (>1753 m) Navajo Sandstone as the zone of highest affinity. The seemingly high overlap of these models can be clarified by examining environmental data recorded at the plot scale: among plots mapped to Navajo Sandstone, Slickrock affinity was positively correlated with percent rock cover (Spearman's rho=0.50) while Upland Sands affinity was negatively correlated (Spearman's rho=-0.15). The Upland Sands group also differed from Slickrock in its high affinity for eolian deposits and its lower affinity for canyon bottoms and cliff bases within the Navajo/Temple Cap/eolian zone (Fig. 2.8-2.9). However, below this zone on the southwestern side of Zion the Upland Sands group had higher affinity for slopes adjacent to Navajo Sandstone cliffs than more distant lowlands below 1423 m (Fig. 2.9).

The coalition group with highest affinity for the steep sloping terrain below Navajo Sandstone cliffs was given the name 'Rocky Slopes'. *Fraxinus anomala*, *Erigeron utahensis*, *Poa fendleriana*, and *Quercus turbinella* are prominent members of this group (Table 2.2F). The first split of the Rocky Slopes regression tree model identifies substrate as an important affinity predictor, with lower affinity for Carmel, alluvium, colluvium, eolian, lacustrine and residuum than for other substrates (Fig. 2.10). This data split may actually reflect the influence of slope more than substrate characteristics *per se*, given that this set of six substrates has a lower mean slope (22^{o}) than the remaining ten substrates (61^{o}). Rocky Slopes affinities are lowest at the park's lowest elevations (<1327 m) and highest elevations (> 2321-2368 m) (Fig. 2.10) which suggests a mid-elevational optimum for this species group but may also reflect the fact that terrain at both these elevational extremes is relatively flat. Rocky Slopes affinity is also low in the deep canyon zone (TPI at 100 m radius < 35) (Fig. 2.10) where Crevice Canyon affinity is high (Fig. 2.7) but remains high in other topographic lows adjacent to cliffs. The highest Rocky Slopes affinities are associated with the Kayenta formation which is particularly extensive in the Taylor Creek thrust fault area of northwestern Zion (Fig. 2.10). The broad zone of relatively high affinity above, below and around the Kayenta formation can be attributed to the broad distribution of several members of the Rocky Slopes group, including *Poa fendleriana*, *Amelanchier utahensis* and *Arabis perennans*. These species occupy a wide range of environments at Zion but form a coalition with more narrowly distributed species such as *Shepherdia rotundifolia* (Table 2.2F).

The Rocky slopes group shares three coalition species (*Opuntia macrorhiza*, *Senecio multilobatus* and *Erysimum asperum*) with the Upland Sands group and three others (*Pinus monophylla*, *Juniperus osteosperma* and *Gilia inconspicua*) with the lower-elevation Arid Lowlands group (Table 2.2G). *P. monophylla* and *J. osteosperma* are well-known dominants of Great Basin woodlands and epitomize the Great Basin affinities of many of the Arid Lowlands coalition species. Other coalition species of this group, including *Coleogyne ramossima, Baileya multiradiata* and *Eriastrum eremicum*, have geographic affinities for the Mojave Desert and/or lower-elevation Colorado Plateau rather than the Great Basin (Welsh et al. 2003). Included in this mixture is the common Mojave Desert invasive species *Bromus rubens* as well as its Great Basin counterpart

Bromus tectorum. *Gutierrezi*a spp. (*G. sarathrae* and *G. microcephala*), indicators of grazing disturbance history (Welsh et al. 2003), also have high affinity to the Arid Lowlands group (Table 2.2G).

The arid character of sites occupied by the Arid Lowlands group is verified by its regression tree model which indicates higher affinity for sites below 1596 m elevation, precluding sites such as deep canyons with TPI (100 m radius) less than -22 (Fig. 2.11). Within this low-elevation zone the Arid Lowlands group has lower affinity for substrates associated with riparian areas (alluvium and lacustrine) as well as substrates concentrated at higher elevations (Kayenta, talus, Navajo and eolian) except where these substrates are highly exposed (exposure>215). At elevations between 1596-1818 m the Arid Lowlands group likewise has higher affinity for more exposed sites (exposure>130) (Fig. 2.11) where the moisture/temperature regime is presumably similar to lower elevations.

Another low-elevation species group named ‘Lowland Flats’ had high affinities for sites below 1388 m, especially alluvium and Moenkopi substrates with TPI (50 m radius) greater than -0.5 (Fig. 2.12). In Zion Canyon these conditions correspond with floodplains and benches above the zone where the Streambank group is concentrated (Fig. 2.5). These portions of Zion Canyon have been subject to intensive agriculture in the past and bear the marks of this land use history. A combination of native species (e.g., *Lycium pallidum*, *Atriplex canescens*, *Sphaeralcea grossulariifolia*, *Elymus smithii*) and exotics associated with disturbance (*Erodium circutarium*, *Tragopogon dubius*, *Lactuca serriola*) typified the Lowland Flats group (Table 2.2H). Various combinations of these species also occurred throughout the low elevation zone in Zion. Above 1388 m elevation, higher affinities were associated with flatter areas (slope <6^o) on mostly unconsolidated substrates (Fig. 2.12).

Coalition Clustering yielded two groups associated with the Carmel formation that caps the Navajo Sandstone on the eastern and northern sides of Zion. One group (Mesic Mesa Top) is interpreted as indicating slightly more mesic settings than the other group (Xeric Mesa Top). Highest affinities for both groups are found in a zone defined by the Carmel formation above 1791 m, but outside of this zone the Mesic Mesa Top group's affinities are shifted toward higher elevations than Xeric Mesa Top's (Fig. 2.13-2.14). The Mesic Mesa Top group had high affinities for the residuum deposits that in many places cap the Carmel, but lower affinities for the Navajo and eolian substrates that occur below the Carmel, and lowest affinities below 1486 m (Fig. 2.13). The Xeric Mesa Top group, in contrast, did not have exceptionally high affinity for residuum, did not have lower affinity for Navajo or eolian than for other non-Carmel substrates, and reached its lowest measurable affinity only at exposed sites (exposure>129) below 1430 m (Fig. 2.14).

Although the Mesic and Xeric Mesa Top groups share a set of prominent woody species (*Pinus edulis*, *Quercus gambelii*, *Amelanchier utahensis* and *Peraphyllum ramosissimum*) as well as two herbaceous species (*Carex rossii* and *Swertia radiata*), the affinity order of these species is almost exactly reversed for the two groups (Table 2.2I-J). *P. ramosissimum* and *S. radiata* have higher affinity for Mesic Mesa Top than *P. edulis* and *C. rossii* (Table 2.2I) while the opposite is true for Xeric Mesa Top (Table 2.2J). Other species that do not overlap these groups include *Viola purpurea*, *Cercocarpus montanus*, *Pachystima myrsinites* and *Mahonia repens* of Xeric Mesa Top and *Lathyrus lanszwertii*, *Balsamorhiza sagittata*, *Phlox longifolia*, *Penstemon linarioides* and *Purshia tridentata* of Mesic Mesa Top (Table 2.2I-J). Only two members of these groups overlap with other groups: *Symphoricarpos oreophilus* links Mesic Mesa Top to the High Plateau group (Table 2.2B) and *Amelanchier utahensis* links both Mesa Top groups to the Rocky Slopes group (Table 2.2F).

Affiliate Species of Coalition Groups

Species with the highest affiliation to coalition groups (affiliate species) corresponded only loosely to the species with highest affinity (coalition species) (Table 2.2, Appendix 2.2), reflecting the different patterns emphasized by affiliation and affinity values. Affiliation (percent co-occurrence) was much more a reflection of a species' total frequency than affinity (mean phi). With the exception of the Streambank and Rocky Slopes groups, less than half each group's affiliate species were also coalition species. The number of affiliate species (species density: a reflection of species richness in plots where coalition species are concentrated) ranged from 21 for the Xeric Mesa Top group to 27 for Crevice Canyon (Table 2.2). Although the number of affiliate species per group was in most cases higher than the number of coalition species, the total number of affiliate species (101) was lower than the coalition species total (173), reflecting the greater inter-group overlap of affiliate species.

As a general pattern, the most widely-distributed species had the highest affiliation values and were affiliated with the most coalition groups. *Poa fendleriana*, the most frequently encountered species at 190 occurrences, was an affiliate of all ten described groups. Other widely-distributed species with multiple affiliations include

Quercus gambelii, *Amelanchier utahensis*, *Bromus tectorum*, *Arabis perennans*, *Senecio multilobatus* and *Opuntia macrorhiza*. In each of these cases the species was affiliated with several additional groups beyond the one(s) where it belonged as a coalition species. Conversely, coalition species with few occurrences were generally affiliated with fewer groups, in many cases none at all. Some moderately frequent species, including *Artemisia ludoviciana*, *Artemisia tridentata*, *Elymus elymoides*, *Eriogonum racemosum*, *Machaeranthera canescens*, *Phacelia heterophylla*, *Sporobolus cryptandrus*, *Stipa comata*, *Stipa hymenoides* and *Yucca angustissima*, have the distinction of emerging as affiliate species without belonging to any of the coalition groups. The latter is also true of *Artemisia* sp., *Melilotus* sp. and *Oenothera longissima* which were excluded from entering coalition groups because of having only two occurrences, but nevertheless emerged as affiliates of the Streambank group.

Weighted mean cover ranged from a fraction of a percent for most affiliate species (Table 2.2) to 23 percent for *Quercus gambelii* with the High Plateau group (Table 2.2B), followed closely by *Bromus tectorum* with the Lowland Flats group at 18 percent (Table 2.2H). These percentages are lower than might be expected based on the maximal cover recorded for these species in these environments, but reflect average cover across plots where coalition species were concentrated. Although cover values in Table 2.2 are not strictly comparable with conventional discrete plot averages, they can be used in a similar way to quantify relative differences in species dominance. Species with a mean cover value of two percent or more could be construed as dominant species and are underlined in Table 2.2. Most of these species were also recognized as dominants in previous analyses of the BYU-RMRS dataset (Harper 1993, Harper et al.

1993, 2001, 2003), although dominant species are not as clearly segregated among coalition groups as they were for previously-defined vegetation types. For example, *Pinus ponderosa*, which defined the Ponderosa Pine vegetation type in Harper et al. (2001), emerged as a dominant affiliate species of four coalition groups (Xeric and Mesic Mesa Top, Upland Sands and Slickrock). Many of the dominant species at Zion appear to be generalists that can achieve dominance in a variety of different environments with a variety of different subordinate species.

Correspondence with Previously-described Vegetation Units

To a certain extent, the ten species groups obtained through coalition clustering mirrored the ten vegetation types previously described by Harper et al. (2001). Table 2.3 summarizes the correspondence between species groups and vegetation types in terms of group affinities of modal species described for each type (see also Appendix 2.3). In Table 2.3, vegetation types (rows) and species groups (columns) are arranged such that high values follow roughly the diagonal.

Some species groups were compositionally very similar to modal species of specific vegetation types, e.g. seven of the nine coalition species of the Lowland Flats group were modal species of the Abandoned Fields type (Table 2.3, Appendix 2.3). Other species groups and modal species sets resembled one another but the correspondence was not as strongly one-to-one; e.g. Arid Lowlands and Blackbrush, Slickrock and Rock Crevice, High Plateau and Douglas/White Fir, Streambank and Riparian (Table 2.3). The Upland Sands group had high correspondence with three vegetation types (Ponderosa Pine, Mountain Brush, and Rock Crevice) as did Crevice

Canyon (Riparian, Douglas/White Fir, and Hanging Gardens) and the Mesa Top groups (Douglas/White Fir, Ponderosa Pine and Juniper-Pinyon). The Sagebrush vegetation type had relatively weak affinities with the Arid Lowlands group compared to the stronger affinities between the latter and Blackbrush.

Few of the rarer species at Zion were listed as modals in Harper et al. (2001) because of the requirement that modal species also be prevalent. Also, the modal species concept followed by Harper et al. (2001) did not accommodate species modality in multiple vegetation types, unlike the coalition clustering approach which highlighted bimodal and (in the case of *Amelanchier utahensis*) tri-modal memberships in species groups. While these methodological details account for some of the differences between Harper et al. (2001) and the results presented here, other differences can be attributed to the fundamentally different ways in which the two approaches partitioned species distribution variation at Zion. The discrete, dominant-species based classification followed by Harper et al. (2001) masked some of the floristic distinctions and gradations captured by the species group approach, such as the subtle floristic contrast between the Xeric and Mesic Mesa Top groups and the floristic continuity of the Arid Lowlands group.

Because dominant species and growth forms such as ponderosa pine, juniper-pinyon and mountain brush occupy multiple environmental settings at Zion, their use as classification criteria by Harper et al. (2001) led to environmentally ambiguous vegetation types. Some of these ambiguities were clarified in a subsequent manuscript (Harper et al. 2003) that split the juniper-pinyon vegetation type into three subtypes: a higher elevation subtype containing *Pinus edulis* (like the Mesa Top groups), a mid-elevation subtype with *Pinus monophylla* (like Rocky Slopes) and low-elevation subtype with *Juniperus osteosperma* but no *Pinus* (like Arid Lowlands). Cogan et al. (2004) differentiated pinyon-juniper vegetation in a similar way at the alliance level (Appendix 2.4).

The NVCS associations and alliances described for Zion by Cogan et al. (2004) are more finely divided than the vegetation types of Harper et al. (2001), although they can be lumped into a comparable number of higher units. The NVCS hierarchy provides one way of lumping associations and alliances based on a set of standardized criteria. The highest NVCS level (formation class), based on gross physiognomy, is represented at Zion by six classes: forest, woodland, shrubland, dwarf shrubland, herbaceous and sparse vegetation. As shown in Table 2.4, I used these classes to generalize compositional affinities between coalition groups and NVCS associations, which are presented in greater detail in Appendix 2.4.

Table 2.4 can be interpreted in two ways; on one hand, it indicates the relative proportions of different physiognomies associated with each coalition group, and on the other hand it summarizes the environmental affinities of the associations in each physiognomic class. From the latter perspective, the forest class has higher elevation/mesic affinities (e.g., High Plateau, Crevice Canyon, Streambank) while woodland, shrubland, dwarf-shrubland and sparse vegetation have lower elevation/xeric affinities (Rocky Slopes, Arid Lowlands, Lowlands Flats) and the affinities of herbaceous vegetation follow their own pattern (Streambank, Rocky Slope, Arid Lowlands). Upon closer examination of individual associations (i.e. Appendix 2.4), one finds that these general patterns belie considerable variation. Shrublands, for example, include high elevation associations such as Mountain Snowberry/Kentucky Bluegrass and Strapleaf Willow/Beaked Sedge as well as the expected low elevation units such as Blackbrush and Four-wing Saltbush (Appendix 2.4).

The limited environmental interpretability of NVCS physiognomic classes at Zion led me to seek a more natural higher classification based on coalition group affinities. Using the affinity table presented in Appendix 2.4, I carried out a hierarchical cluster analysis that grouped associations in a more environmentally interpretable way. This analysis revealed clusters of associations representing certain physiognomic combinations in certain environmental settings (Fig. 2.15). The fourteen clusters highlighted in Figure 2.15 were named for their environmental (i.e. coalition group) affinities and physiognomic composition. These clusters are nested in three major groups with primary affinities for (1) Lowland Flats, Arid Lowlands, and Rocky Slopes; (2) Mesa Top, Upland Sands and Slickrock; and (3) Streambank, Crevice Canyon and High Plateau (Fig. 2.15). Some associations did not fit neatly within this classification scheme, e.g. Green Rabbitbrush/Kentucky Bluegrass Semi-natural Shrubland was a outlier to the Lowland Flats/Arid Lowlands/Rocky Slopes clusters; Needle-and-Thread Great Basin Herbaceous Vegetation was an outlier to the Crevice Canyon/High Plateau clusters, and Rocky Mountain Juniper--Gambel Oak Woodland was anomalously positioned next to the Streambank clusters (Fig. 2.15). Some of these outliers may be associations sampled by the USGS-NPS survey that were missed or poorly captured by the BYU-RMRS survey.

A reclassification exercise was also carried out for the USGS-NPS vegetation map units. Various higher classification schemes accompanied this map, including the eight-class scheme shown in Table 2.5. These classes are more environmentally-descriptive than the NVCS formation classes because they distinguish between higher and lower elevation forests and shrublands, riparian and non-riparian zones, and slickrock as opposed to other bare soil/stone formations. Nevertheless, an even more descriptive classification (Fig. 2.16) was achieved through hierarchical clustering using affinities between vegetation map units and coalition group affinity maps (Appendix 2.5). The map unit clusters (Fig. 2.16) resembled association clusters (Fig. 2.15) in a general way, but map units were more strongly clustered by elevation and spatial proximity, as might be expected because of the spatial basis of the analysis. A cluster with High Plateau affinities (Higher Elevation Forest/Shrub/Herb) was linked to clusters with Mesa Top affinites (Higher Elevation Sparse, Higher Elevation Woodland/Shrub/Herb) rather than the cluster with Streambank affinities (Lower Elevation Riparian). Map units with Slickrock and Upland Sands affinities formed a tight cluster closely linked to a Crevice Canyon unit (the Douglas Fir Forest Alliance). The Lower Elevation Talus/Slope and Sparse/Shrub/Herb clusters parallel the Rocky Slopes and Arid Lowlands/Lowland Flats groups respectively. Lowland Flats affinities are also high for the Lower Elevation Disturbed cluster that contains a single map unit, Cheatgrass Annual Disturbed Grassland. I also assigned the name ‘Lower Elevation Sand’ to an anomalous cluster mixing riparian and upland sand substrates. Another anomaly involves Fremont Cottonwood-Velvet Ash Woodland, which was positioned near the Lower Elevation Sparse/Shrub/Herb cluster rather than the Riparian cluster, possibility because of inaccuracies in one or both of the map types being compared.

DISCUSSION

This paper has described how plant species groups were identified at Zion National Park using a clustering technique (coalition clustering) that quantifies the degree of affinity of each species to each group and allows species to belong to multiple groups. I asserted that these species groups (coalitions) are essentially faithful species according to an individualistic definition of community fidelity. Individualistic equivalents of constant species, defined as species that tend to co-occur with species groups, were also presented (affiliate species), and the relative dominance of these species was quantified. Because coalition species groups could be readily interpreted as species with similar environmental affinities at Zion, providing insights beyond previous vegetation studies, I conclude that the individualistic species group approach was an effective alternative to vegetation classification for characterizing community and environmental variation.

My discussion centers around the two main features of the individualistic species group approach that set it apart from previous plant community characterization studies at Zion. The individualistic species group approach (1) models spatial community variation continuously rather than discretely, and (2) gives species equal weight rather than weighting dominant species more heavily. Taking this approach does not preclude the possibility that relatively discrete patterns may be present, or that dominant species may be important determinants of community composition, but it does allow these possibilities to be actually examined rather than merely assumed.

Community Continuity and Discreteness

Gleason’s individualistic concept (Gleason 1926, 1939) contributed to the later development of the community continuum concept by workers such as Curtis (1959), Goodall (1963), McIntosh (1967) and Whittaker (1967). Taken to its logical extreme, the continuum concept postulates that species distributions bear no relationship to one another, resulting in communities lacking any kind of natural boundaries (Leibold and Mikkelson 2002). However, as pointed out earlier in this paper, Gleason tempered his views of community continuity with an acknowledgement that relatively discrete community patterns can often be recognized and are worthy of description and study (Gleason 1926, 1939). I have also pointed out that Curtis (1959) described communities in discrete terms for practical, heuristic reasons. The reality of (relatively) discrete community patterns and the utility of discrete community descriptions provide rationale for the individualistic species group approach followed here.

The individualistic species group approach addressed two types of patterns—species distributions and site composition—from two perspectives—discrete and continuous. Beginning with a discrete species perspective, groups of species with similar distribution patterns were identified through cluster analysis. Continuous species patterns were then added through species affinity calculations, then translated to continuous site patterns though weighted averaging at the plot scale. Finally, discrete site patterns were introduced through regression tree modeling which grouped sites sharing similar affinity values in similar environments. Spatial discreteness was thus relegated to a side effect of the final modeling step, rather than a primary feature of the community model.

What do these results tell us about community discreteness in the Zion landscape? One would expect that the sharp transitions visible in the topography and some of the substrates would be natural boundaries for plant distributions. Regression tree models of coalition group affinities support this supposition in several instances. Narrow canyons and riparian zones define rather discrete high-affinity zones for the Crevice Canyon (Fig. 2.7) and Streambank (Fig. 2.5) coalition groups, as does the Navajo Sandstone for Slickrock and Upland Sands (Fig. 2.8-2.9). The zone of steep Navajo Sandstone cliffs appears as a dividing line in several regression tree models; for example, the elevational splitting point indentified in the first data split of the Arid Lowlands coalition group (1596 m) lies at approximately the base of the lower Navajo Sandstone cliffs in the main section of the park (Fig. 2.11), while the first split of the Mesa Top groups (1791 m) lies near the top of this same set of cliffs (Fig. 2.13-2.14). This pattern breaks down, however, in the Kolob (northwestern) section of Zion where the Navajo Sandstone cliffs occur at a higher elevation than these data splitting lines. It would appear that main body of cliffs forms a natural break in the landscape detectable through regression tree modeling, but that the real factor involved is elevation, not the cliffs in and of themselves.

Austin and Smith (1989) pointed out that discrete community patterns are likely to be most evident in landscapes where extensive areas of similar environment are separated by narrow environmental transition zones—as appears to be the case for Zion. They then made a distinction between community patterns due to such landscape properties and continuum patterns due to underlying environmental gradients. If species are arranged along uniformly-scaled gradients, they argued, co-occurrence patterns should dissolve into continuous compositional gradients (Austin and Smith 1989). This model assumes, however, that all areas of the environmental space are equally likely to be occupied, and that species are fully independent in terms of their ecological attributes. Countering this assumption, one might expect some species to be spatially clustered even in the absence of sharp environmental transitions due to phenomena such as phylogenetic niche conservatism (Webb et al. 2002) or positive ecological interactions (Callaway 1997). These phenomena can be accommodated by the individualistic concept because they fall under the category of “similarity in the contributing causes” leading to “the recurrence of a similar juxtaposition [of plant species] over tracts of measurable extent” as described by Gleason (1926, p. 25). In these cases (niche conservatism and ecological interactions) the contributing causes are species properties, not landscape properties.

Gleason (1926) invoked migration (dispersal history) and environmental selection as the primary causes of species distributions. To the extent that these causes are unique for each species, continuous community patterns will be manifest; to the extent that they are similar, discrete patterns are possible. This paper has focused on environmental causes of species distributions at Zion, but dispersal history undoubtedly also plays a role. Idiosyncrasies of dispersal can result in species being absent from portions of their optimal environment or disproportionately frequent in suboptimal environments (Shmida and Wilson 1985, Dunning et al. 1992, Nekola and White 1999). If barriers or facilitators of dispersal affect multiple species in a similar way, common distribution patterns may arise yet show little relationship to environmental variables. Such multi-species dispersal effects could have contributed to observed species association patterns at Zion, but examining such effects lies beyond the scope of this study. For current purposes, dispersal effects are considered noise that weakens the species-environment relationships of interest.

Coalition Clustering Effects

Uncommon species that do not occupy all sites of suitable habitat are one of the primary sources of dispersal-related noise in community datasets. The coalition clustering technique partially compensates for this type of noise by linking species having overlapping distributions without requiring that all species overlap in the same way. In many cases, species belonging to the same coalition group at Zion did not actually co-occur in any plots, but the negative pairwise associations of these species were overridden by their shared positive associations with other species belonging to the group. Species occurring in many plots appeared to provide some of the “glue” that held species occurring in fewer plots together in the same group.

The phi coefficient of association likely accentuated the tendency toward diffuse overlap within coalition groups. Because phi incorporates joint absence information, it is less sensitive to differences in species frequency than presence-only coefficients such as the Jaccard index (Jackson et al. 1989, Sanderson et al. 2006). Species clustering based on presence-only coefficients tends to group species based on their frequency unless additional standardization steps are followed (Austin and Belbin 1982, Jackson et al. 1989, McCune and Grace 2002). In contrast, coalition clustering using the phi coefficient yielded species groups containing mixtures of common and rarer species. Species within coalition groups can have variable niche breadths within a diffuse zone of shared niche space. The same can be true of species that are faithful to a community unit, such as the modal species described by Harper et al. (2001), although in this case the niche space is discretely defined.

Because coalition clustering solutions vary depending on the threshold association value defined by the analyst, multiple values may need to be explored to find a solution at the desired scale. In the current application, the selected solution contained a moderate number of clusters with moderate numbers of species each, at a scale that allowed comparison with the vegetation classification of Harper et al. (2001). A more objective method for cluster selection could be implemented by searching across multiple threshold values to find an "optimal" solution in which association is maximized within clusters and minimized between clusters (cf. Sanderson et al. 2006). Similar optimal partitioning procedures have been developed for use with standard clustering algorithms (Aho et al. 2008). Although optimal partitioning has not been tested with coalition clustering, its likely effect would be to select a solution with minimal species overlap between groups. Since overlapping composition contributes to the individualistic character of species groups, this would be an undesirable effect for current purposes. Furthermore, the idea of a single optimal classification solution runs contrary to the pluralistic spirit of the individualistic concept. The coalition groups presented here are but one of many potentially useful and informative clustering solutions.

Another reason why optimal partitioning may have limited relevance for coalition clustering is because a given threshold value does not necessarily mean the same thing for different coalition clusters, depending on their representation in community samples. The two Mesa Top groups, for example, could be differentiated at a threshold value of phi=0.15 because of the relatively large number of plots representing the Carmel

Formation zone. If there had been fewer plots in this zone, a higher threshold value may have been required to distinguish these two groups. The Arid Lowlands group provides another example of how threshold value selection influences coalition clustering results. The emergence of Arid Lowlands as a single group was somewhat surprising given its range of vegetation types and mixture of Mojave Desert and Great Basin species. Exploration of alternative clustering solutions at different threshold values helped to clarify this pattern. Figure 2.17 illustrates an alternative set of two Arid Lowland groups obtained using coalition clustering at phi=0.2. One group containing *P. monophylla* and *J. osteosperma* is recognizable as having higher elevation/Great Basin affinities while the other has lower elevation/Mojave affinities (Fig. 2.17). Nevertheless, these two groups overlap to a considerable degree and the invasive grass *B. rubens* is the highest-affinity species in both of them. Other overlapping species have mostly inverted affinity rank order in the two groups, as illustrated by the lines connecting these species in Figure 2.17. This situation is reminiscent of the inverted affinities of species in the two Mesa Top groups (Table 2.2I-J). Both Arid Lowlands and Mesa Top can thus be characterized as loosely-associated species groups that can be subdivided into overlapping subgroups. Unlike Arid Lowlands subgroups, the Mesic and Xeric Mesa Top groups do not appear to represent species with different geographic affinities, and their ecological significance at Zion deserves further study.

Sampling Issues

One of the drawbacks of coalition clustering, and species clustering in general, is that association patterns are sensitive to the area sampled and sampling strategy. Discrete community units need not be defined, but the decision of how to define and sample the study area remains. In the current application, the use of national park boundaries to delimit the study area makes sense from a political or management perspective but not from an ecological perspective. Zion has artificial boundaries that truncate environmental gradients; the elevation gradient, for example, continues both below Zion in the Virgin River drainage and above on the Markagunt Plateau. Species whose environmental affinities lie primarily outside of such truncated gradients are incompletely characterized in analyses restricted to Zion.

However, given the fact that the National Park was chosen as the study area, the systematic sampling scheme followed by the BYU-RMRS survey was a reasonably unbiased approach for capturing environmental variation within the park. Aside from the unlikely possibility that the ca. 1.6 km distance between plots coincides with periodic environmental variation at Zion, the more-or-less evenly spaced plot arrangement of the BYU-RMRS survey (Fig. 2.2) yielded an area-proportional sample of Zion's environments. Environmental conditions that are more frequent in the landscape were captured with greater frequency by this approach, in contrast to the gradsect sampling strategy followed by the USGS-NPS survey which sought to capture the range of environmental variation without regard for frequency.

The effects of these different sampling strategies are illustrated in histograms showing the proportional correspondence between plots and pixels for the environmental variables used in this study, which corresponded more closely for the BYU-RMRS survey than the USGS-NPS survey (Fig. 2.18-2.19). Even so, the BYU-RMRS dataset had an over-representation of low elevations, low slopes, moderate exposures (Fig. 2.18) and alluvial substrates (Fig. 2.19) that can be attributed at least in part to the non-systematic riparian and old field plots included in the survey. On the other hand, excessively steep or bare plot locations were avoided or adjusted by BYU-RMRS survey crews leading to an under-representation of high slopes and Navajo Sandstone substrates. However, these same patterns of environmental over- and under-representation were present to an even greater degree in the USGS-NPS dataset (Fig. 2.18-2.19). Consequently the BYU-RMRS dataset has a larger, comparatively more representative sample of common environments at Zion (such as the Navajo Sandstone), while the USGS-NPS dataset has better representation of rarer, more unique environments and communities (such as wetlands). In terms of ecological representation, these two datasets can be viewed as complementary.

The merits of systematic or random versus subjective community sampling have been widely debated. In a recent forum (Herben and Chytrý 2007), Lájer (2007) and Chiarucci (2007) stressed the importance of random, statistically-independent samples for rigorous statistical analysis of vegetation patterns, while other authors noted that this level of rigor is not crucial for many vegetation science objectives (Botta-Dukát et al. 2007, Diekmann et al. 2007, Lepš and Šmilauer 2007, Økland 2007, Roleček et al. 2007). A truly random plot arrangement is not only unlikely to capture community variation of interest (Diekmann et al. 2007, Lepš and Šmilauer 2007, Roleček et al. 2007), but is not truly statistically-independent because of spatial autocorrelation (Økland 2007, Ricotta 2007, Wilson 2007). Hence some form of sample stratification, whether spatial, environmental or vegetation-based, is usually required for meaningful community analysis (Økland 2007, Wilson 2007). Adding to this discussion, I note that evenly-spaced systematic plot sampling is a form of spatial stratification that minimizes the effects of spatial autocorrelation as well as the bias of environmental/vegetation stratification schemes. Such a sampling strategy fits well with an individualistic approach that does not require *a priori* decisions concerning which environmental variables are of greatest importance in determining species distributions. Systematic sampling also captures environmental conditions that might otherwise be excluded because of their “transitional” nature, such as the vegetation transitions avoided by the USGS-NPS survey (Cogan et al. 2004).

Differences in sampling strategy between the BYU-RMRS and USGS-NPS surveys pose certain limitations when comparing the patterns they reveal. Species association patterns evident in the BYU-RMRS dataset would not be expected to be quantitatively repeated in the USGS-NPS dataset because of its different sampling distribution, not to mention differences in plot size, taxonomic resolution and the ca. 20-year interval between the two surveys. These considerations dampened the otherwise attractive possibility of using the USGS-NPS dataset to assess the accuracy of the predictive spatial models built using the BYU-RMRS dataset. Such an accuracy assessment was attempted by overlaying validation (USGS-NPS) plots on predictive affinity maps for each coalition group, then comparing map pixel values with affinities based on validation plot species composition. This exercise revealed widespread quantitative differences between validation plot- and predictive map-based affinity estimates suggesting low predictive accuracy of the regression tree models. However, an alternative interpretation is also possible: low predictive accuracy may merely indicate the failure of a subjective dataset (USGS-NPS) to predict affinity patterns in the same way as a systematic dataset (BYU-RMRS). Edwards et al. (2006) present a study relevant to this issue; they found that classification tree models based on a ‘purposive’ sample (subjective, targeting certain species or landscape features) were less accurate in predicting distributions of four lichen species than models based on a random/systematic sample. This raises questions over the appropriateness of trying to assess the accuracy of a systematically-derived model using a subjective validation dataset; such an assessment may best be limited to a qualitative analysis. For the tree models presented here, qualitative model accuracy assessments based on ordinal relationships at each tree node revealed high correspondence between the prediction and validation datasets (i.e., predicted separation of higher vs. lower mean affinity values was replicated at 44 out of 47 regression tree nodes).

Dominant Species, Floristic Patterns and Environmental Interpretations

In addition to being associated with the continuum concept, the individualistic concept has been associated with the idea that interspecific interactions play a minimal role in determining plant community composition (Callaway 1997, Nicolson and McIntosh 2002). Gleason did not actually hold such an extreme view, as evidenced by his references to the controlling influence of dominant plant species over subordinate species (Gleason 1939, p. 104-105; cf. Nicolson and McIntosh 2002). However, Gleason challenged the notion that structural dominants are the primary factor controlling community composition at all locations, or that all species are equally affected by their influence:

> Under the individualistic concept, the fundamental idea is neither extent, unit character, permanence, *nor definiteness of structure*. It is rather the visible expression, through the juxtaposition of individuals, of the same or different species and either *with or without mutual influence*, of the result of causes in continuous operation. (Gleason 1926, p. 25, emphasis added)

In contrast, the controlling influence of dominant species was a central theme of Clements' (1916, 1936) organismal community concept:

> Hence, the essential unity of a climax is to be sought in its dominant species… Their reactions and coactions are the most controlling both in kind and amount, and thus they determine the conditions under which all the remaining species are associated with them. (Clements 1936, p. 255)

Given that Clements was here referring specifically to climax vegetation, and was not ignorant of other factors affecting community composition (cf. Eliot 2007), he was not suggesting that dominant species are the primary determinants of community composition under all circumstances. My purpose in quoting Clements is to portray a perspective that provides rationale for the widespread assumption that dominant species should be granted particular emphasis in plant community characterization. I use Gleason's individualistic concept as a counter perspective justifying the purely floristic emphasis of the species group approach, in which dominance is relegated to a secondary descriptor status.

The distinction between community characterization approaches that emphasize dominant species and those that do not is illustrated by Harper et al. (2001) in comparison with the current individualistic species group analysis. Harper et al. (2001) began with a set of vegetation types defined more or less by dominant species and vegetation structure. Prevalent species were then identified for each vegetation type and modal species were derived from the prevalents. The sequence of community characterization thus progressed from dominant to constant (prevalent) to faithful (modal) species. Constant and faithful species in this instance became indicators of the vegetation types, constrained by the dominant species emphasis of the classification. In contrast, the current analysis began by identifying coalition (faithful) species, then affiliate (constant) species, and finally dominant affiliates. This reversal changed the role of faithful species from constrained indicators to unconstrained community descriptors, and changed constants and dominants to secondary descriptors. Dominant species became, in essence, potential explanatory variables for floristic community patterns. The current approach thus bears a conceptual resemblance to unconstrained ordination or indirect gradient analysis (Whittaker 1967, Kent and Coker 1992, McCune and Grace 2002), while the approach followed by Harper et al. (2001) resembles constrained ordination in the sense that the 'environmental' variable of species dominance was imposed *a priori*.

The classification hierarchy of the NVCS can also be viewed as a constrained model in which lower floristic classes are forced into higher physiognomic ones. The incongruence of this classification strategy has been recognized and a revised system that merges floristics and physiognomy more seamlessly has recently been proposed (Faber-Langendoen et al. 2009). A related effort has established a set of "ecological systems" and "ecological divisions" comprised of NVCS associations occupying similar environments (Comer et al. 2003, Comer and Schulz 2007). The seven ecological divisions occurring at Zion (Forest and Woodland, Herbaceous Wetland, Savanna and Shrub-steppe, Sparsely Vegetated, Upland Grassland and Herbaceous, Upland Shrubland, Woody Wetlands and Riparan) (NatureServe 2007) resemble to a certain degree the coalition-group-affinity-based ecological/physiognomic groupings presented in Fig. 2.15-2.16, but the latter provide greater specificity in terms of environments found within the park. While more ecologically-informative than the pre-existing NVCS physiognomic hierarchy, both ecological systems and the new hierarchy are built primarily around structural dominant based descriptors.

Even at the floristic levels of the NVCS (association and alliance), vegetation classification and mapping at Zion emphasized dominant species and followed a constrained analysis approach. Cogan et al. (2004) describe a series of multivariate analyses that guided the classification process, in which species appear to have been weighted by their abundance (cover). Although all species contributed information, dominant species were awarded particular attention and served as the primary criteria for differentiating associations (Cogan et al. 2004, Appendix E). Dominant species likewise played an important role in the mapping process as the primary contributor to aerial photo vegetation signatures, although other visible features related to substrate and topography also contributed (Cogan et al. 2004). Pure floristic patterns, though embedded in the classification and mapping system, were constrained by the *a priori* emphasis on dominant species and abiotic environmental variables. In contrast, coalition species groups of the current analysis were not weighted by abundance and were related to environmental variables *a posteriori*, in accordance with the philosophy of letting the species ‘interpret’ the environment from their own perspective (Beals 1984, McCune and Grace 2002). Environmental affinity models for coalition groups demonstrated that floristic variation at Zion can be explained to a considerable degree by abiotic variables without invoking dominant species effects. This does not preclude the possibility that dominant species effects are also influential (and may co-vary with abiotic variables), but it does suggest that dominant species are not the primary determinants of broad-scale floristic patterns at Zion, at least of the kind captured by the current analysis. Further work is needed to more fully characterize the relative importance of abiotic and biotic factors for different species and scales (cf. Chapter 3).

It should be noted that the current analysis de-emphasized dominant species because coalition clustering is an R-mode (species-based) approach and not simply because species presence-absence was used instead of abundance. Presence-absence association coefficients (e.g. phi) can be substituted with correlation coefficients (e.g. Pearson's r) that incorporate abundance information in R-mode (Ludwig and Reynolds 1998), but this does not lead to a dominant species emphasis because abundances become relativized in the process. Abundance information is not necessarily more useful than presence-absence, depending on the scale and objective of the analysis. Presence-absence information proved effective for characterizing species groups at Zion, where environmental/floristic spatial turnover is high, but might not have sufficed in a smaller or more homogeneous area.

Using presence-absence has the effect of broadening the temporal scale of the community pattern detected; in other words, presence-absence patterns are more likely to reflect long-term environmental conditions (e.g., prevailing climate and substrate) than short-term environmental fluctuations or disturbances that affect abundance (Allen and Starr 1982). Fire disturbance appears to fall into the latter category at the scale of the current analysis, inasmuch as two recently-burned (earlier in the same season) plots sampled in 1988 were compositionally, though not structurally, similar to surrounding plots with Mesa Top affinities. Most plots of the 1987-89 survey were recorded as late seral in relation to fire; hence it is difficult to extrapolate these results to early post-fire conditions in general (on the other hand, the 1987-89 survey provides a valuable baseline for evaluating the effects of recent extensive wildfires at Zion). Fire effects are likely to vary by species and location, and although individual fires may qualify as short-term disturbances, a recurring fire regime can take on the form of a long-term environmental condition. Floyd et al. (2000), upon examining fire history of vegetation types in Mesa Verde National Park, Colorado, concluded that more frequent fire over a 150-year time scale partially explains the distribution of mountain brush vegetation (which tends to resprout after fire) in relation to pinyon-juniper vegetation where fire return intervals have been longer. Fire history may have played a similar role in structuring these same vegetation types at Zion, although its role at the floristic level is less certain.

The question of community stability over time is an important theme related to the individualistic concept, and thus deserves comment to round out this discussion. Given that the plant community patterns described in this paper are but snapshots of conditions at a fleeting period in time, to what extent can they be viewed as permanent features of the Zion landscape? Although a precise answer to this question lies beyond the scope of this study, it is clear that communities are dynamic and change of some form or another is to be expected. Plant species distributions in the Colorado Plateau region are known to have shifted during the Pleistocene (Cole 1990, Anderson et al. 1999, 2000, Coats et al. 2008) and are expected to shift in response to projected climate changes during coming decades (Krause 2009).

The general prediction that a warming, drying trend on the Colorado Plateu (Schwinning et al. 2008) should cause species distributions to shift upward in elevation is complicated by individualistic species responses and landscape configuration at Zion (cf. le Roux and McGeoch 2008). Because of the more or less horizontal arrangement of major rock strata at Zion, an elevational climatic shift would decouple current climate-substrate combinations. Three classes of species responses under this scenario can be envisioned: (1) species sensitive to climate, but less sensitive to substrate will shift upward in elevation (dispersal permitting), (2) species sensitive to substrate, but less sensitive to climate substrate will maintain current distributions, and (3) species sensitive to both climate and substrate will disappear from the park to the degree that their required climate-substrate combination becomes unavailable (a fourth category for species responding to factors other than climate or substrate could also be included). Determing which species may fall into these different categories is difficult to judge from correlative environmental modeling, but the current study offers some clues. Species with high affinities for coalition groups that were strongly correlated with elevation (e.g., Arid Lowlands, High Plateau and the Mesa Top groups) have a greater chance of belonging to category 1, while species with high affinities for groups with strong substrate correlations (e.g. Slickrock, Upland Sands) could belong to categories 2 or 3. Since substrate specificity is a critical differentiating factor in this scenario, making species either more or less susceptible to climate change, such species may deserve particular attention and further study.

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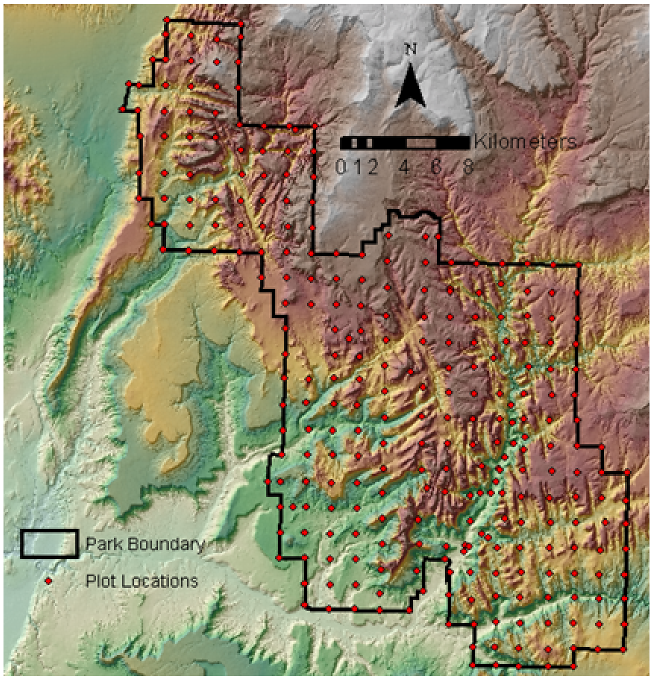


Figure 2.1. Zion National Park, Utah in relation to topography, showing plot locations of the 1987-89 vegetation survey (Harper 1993)

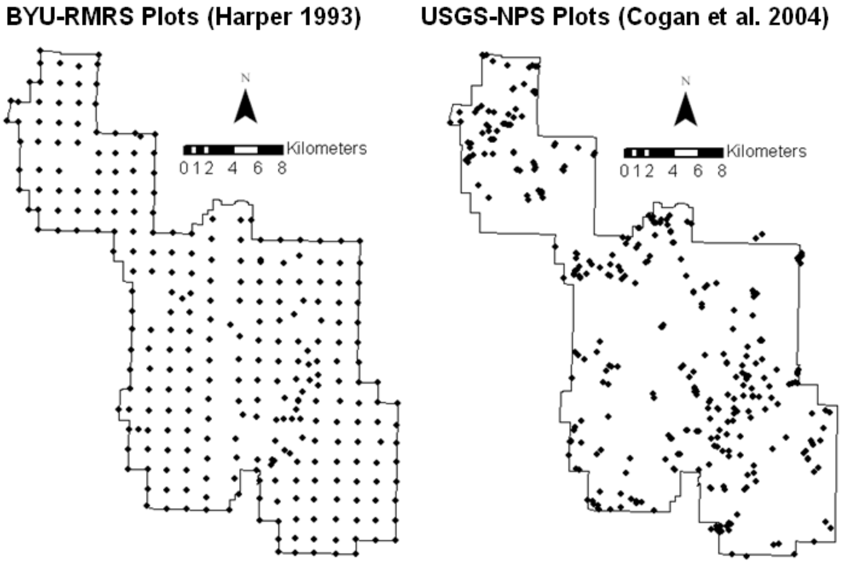
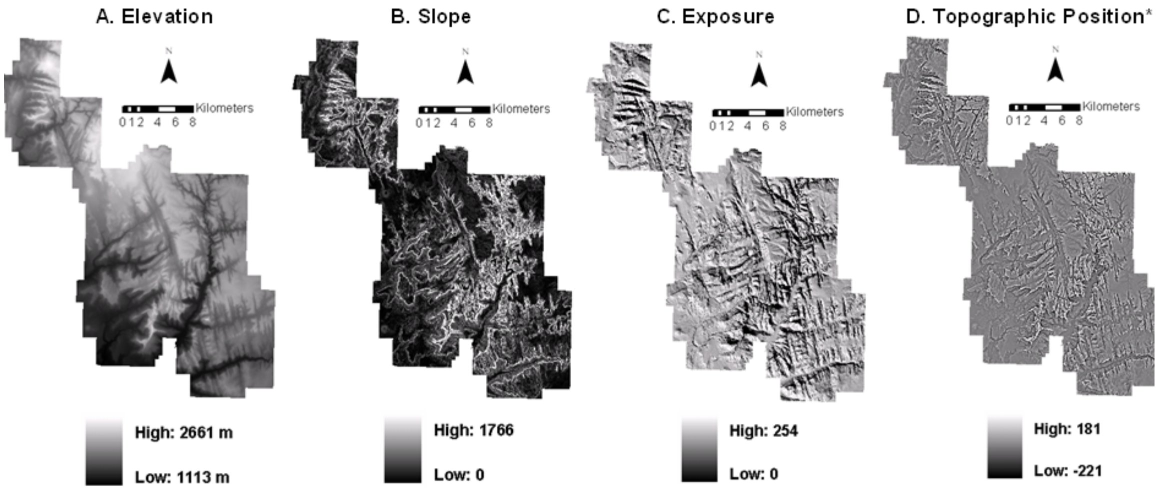


Figure 2.2. Plot locations of two vegetation survey datasets at Zion National Park



*Based on the Topographic Position Index (TPI) at a 50 m radius (Weiss 2001)

Figure 2.3. Abiotic environmental variable layers derived from a 10-m resolution digital elevation model of Zion National Park

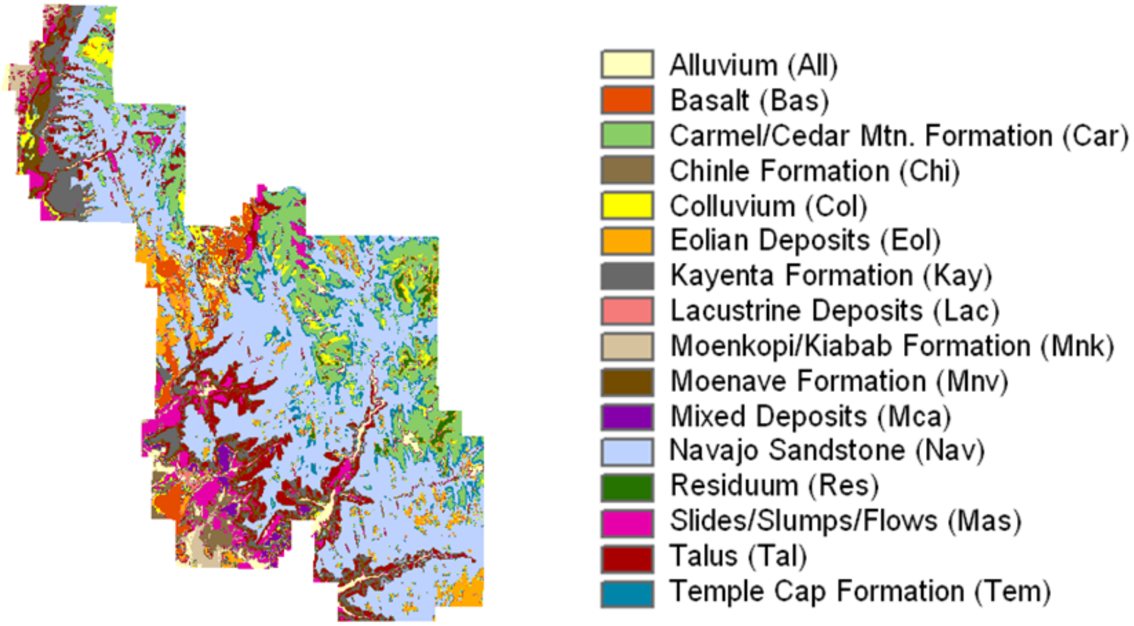


Figure 2.4. Geologic substrate classes derived from a 1:24,000 scale digital geologic map of Zion National Park and vicinity (O'Meara 2006)

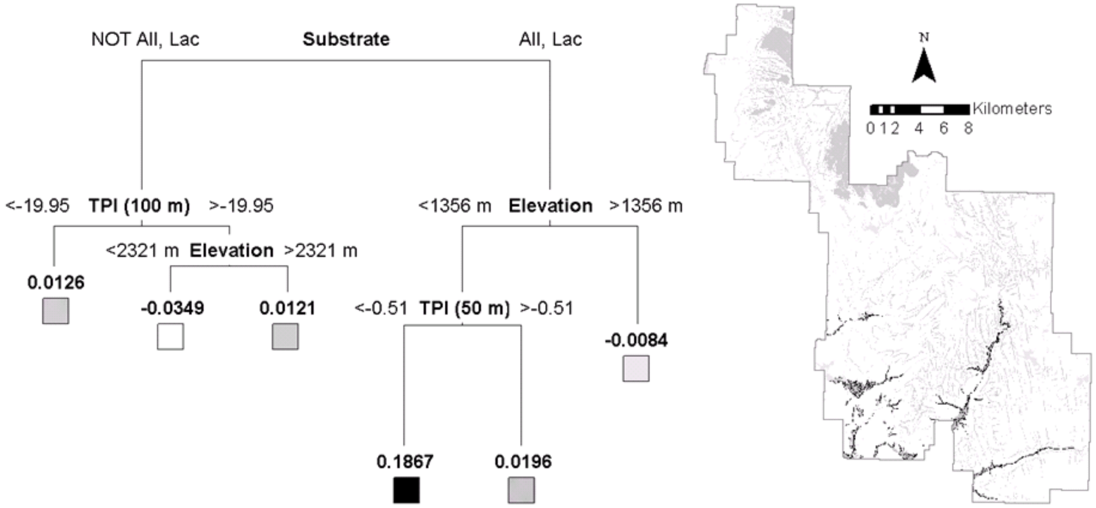


Figure 2.5. Regression tree model and map for the **Streambank** coalition group. Tree model shows relationships between plot affinities and environmental variables (*Substrate: All=alluvium, Lac=lacustrine (see Table 2.1); TPI (50 or 100 m) =Topographic Position Index calculated at 50 or 100 m radius*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

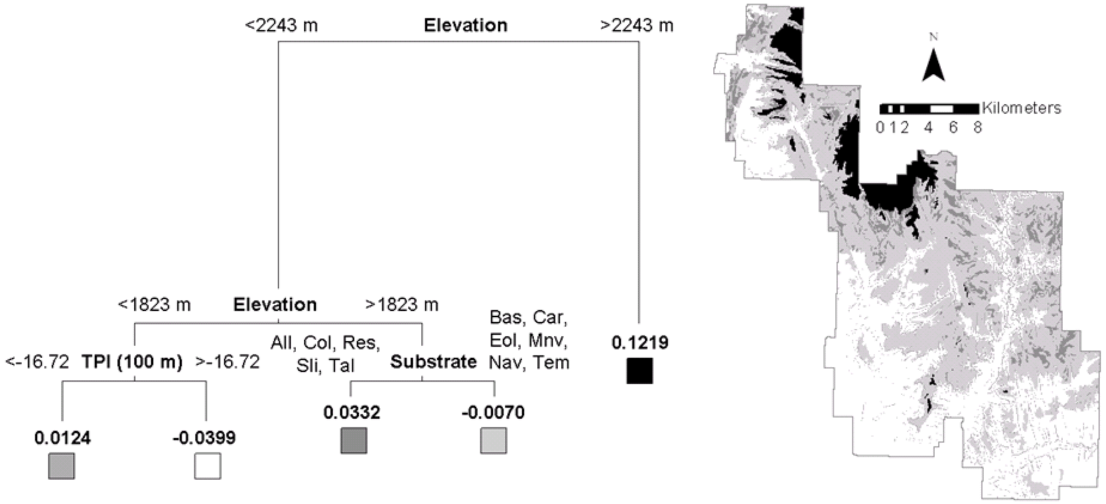


Figure 2.6. Regression tree model and map for the **High Plateau** coalition group. Tree model shows relationships between plot affinities and environmental variables (*Substrate: see Table 2.1 for translation of abbreviations; TPI (100 m) =Topographic Position Index calculated at 100 m radius*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

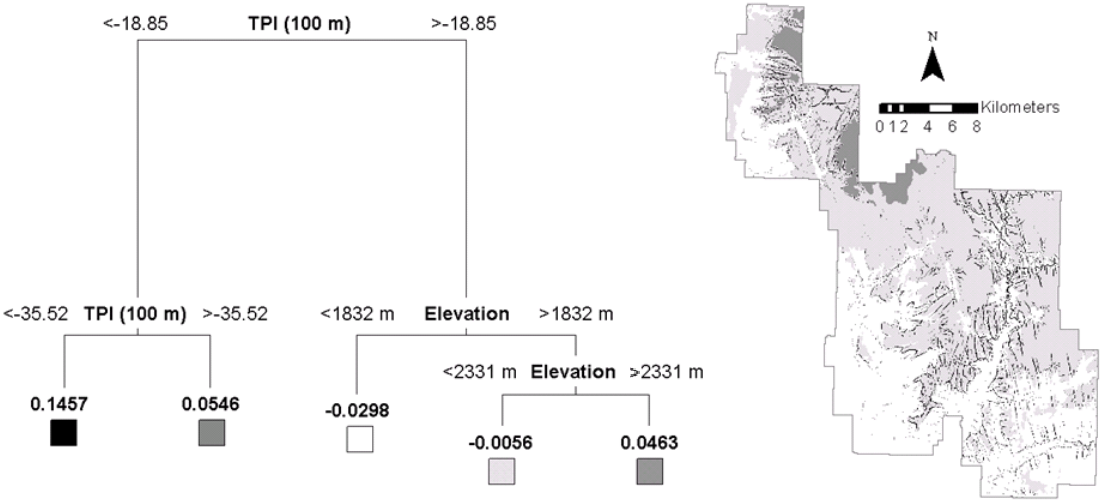


Figure 2.7. Regression tree model and map for the **Crevice Canyon** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*TPI (100 m) =Topographic Position Index calculated at 100 m radius*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

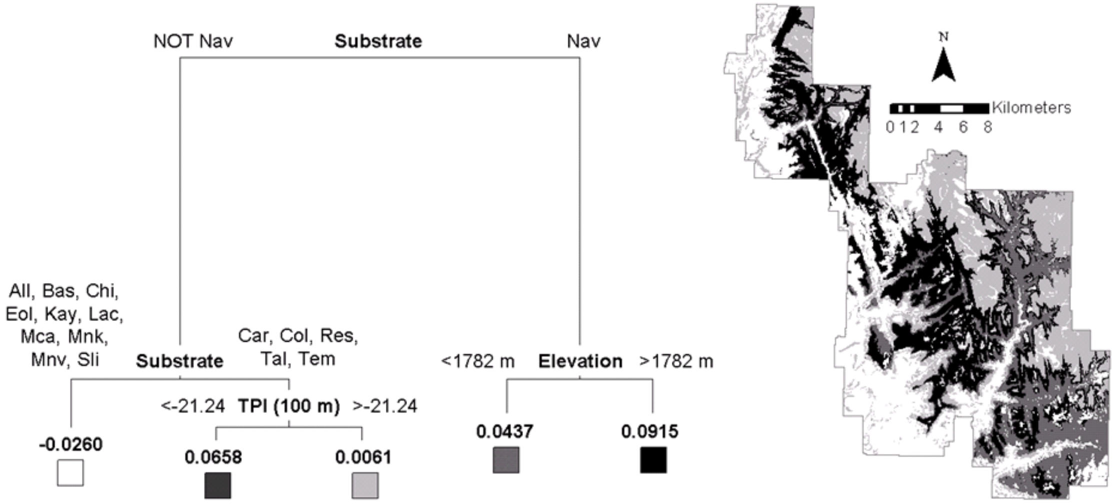


Figure 2.8. Regression tree model and map for the **Slickrock** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*Substrate: Nav=Navajo, see Table 2.1 for translation of other abbreviations; TPI (100 m) =Topographic Position Index calculated at 100 m radius*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

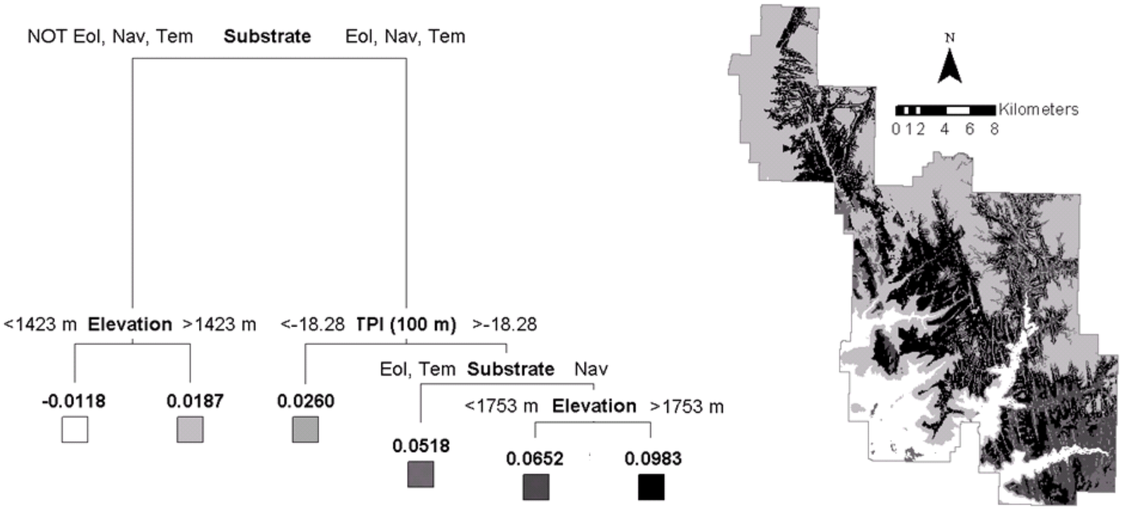


Figure 2.9. Regression tree model and map for the **Upland Sands** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*Substrate: Eol=Eolian, Nav=Navajo Sandstone, Tem=Temple Cap, see Table 2.1; TPI (100 m)=Topographic Position Index calculated at 100 m radius*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

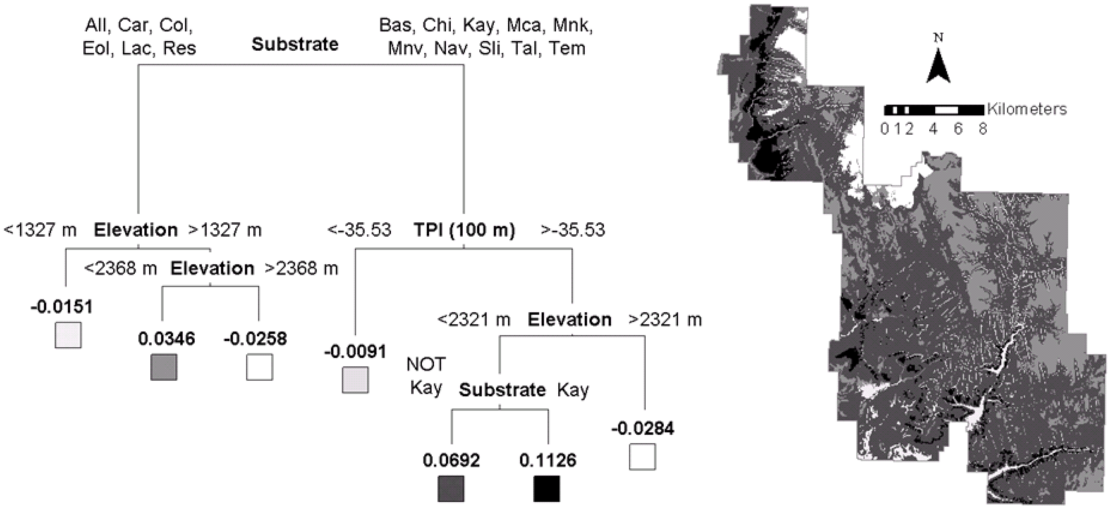


Figure 2.10. Regression tree model and map for the **Rocky Slopes** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*Substrate: Kay=Kayenta, see Table 2.1 for translation of other abbreviations; TPI (100 m)=Topographic Position Index calculated at 100 m radius*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

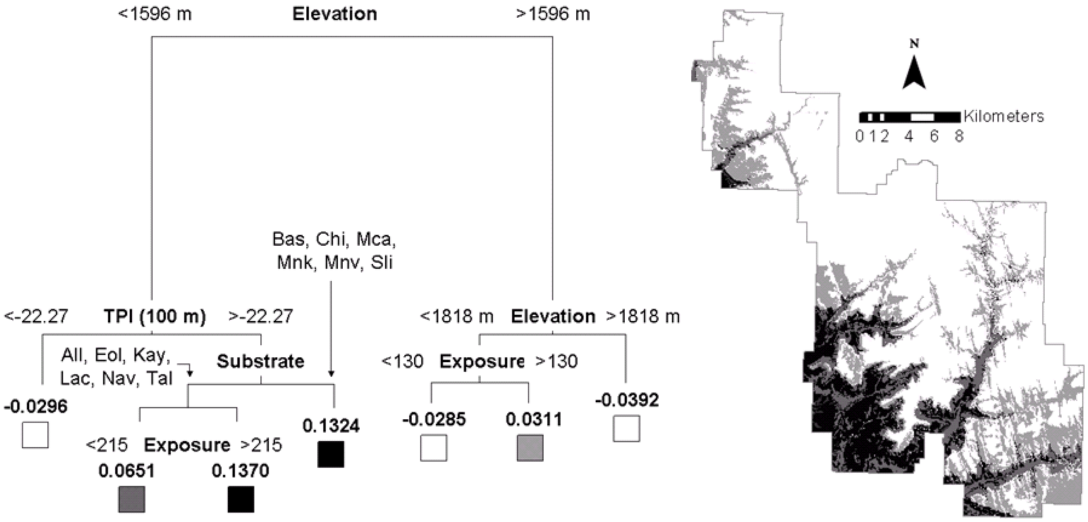


Figure 2.11. Regression tree model and map for the **Arid Lowlands** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*Substrate: see Table 2.1 for translation of abbreviations; TPI (100 m) =Topographic Position Index calculated at 100 m radius; Exposure=solar hillshade at 215^o azimuth and 45^o altitude*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

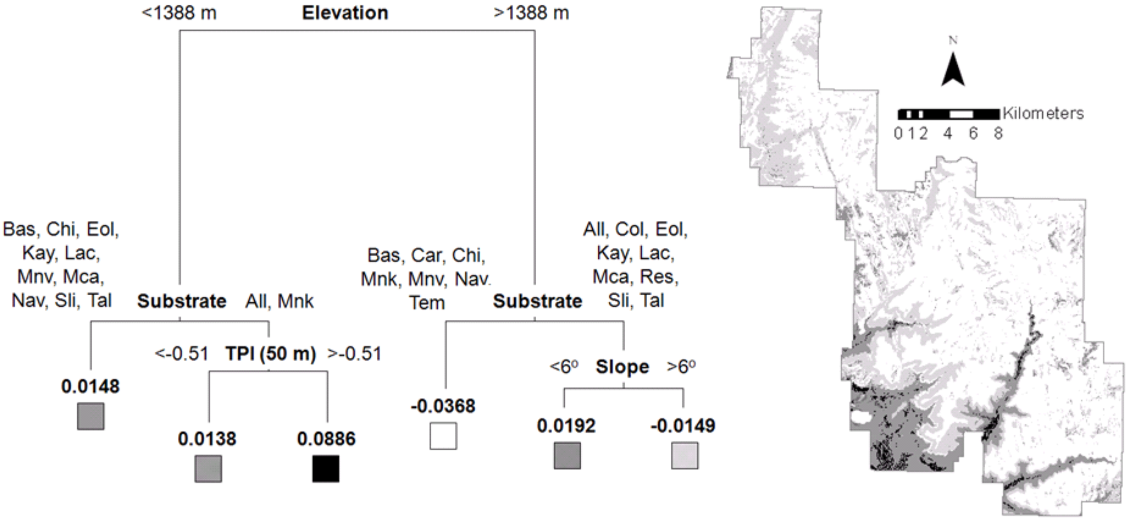


Figure 2.12. Regression tree model and map for the **Lowland Flats** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*Substrate: see Table 2.1 for translation of abbreviations; TPI (50 m) =Topographic Position Index calculated at 50 m radius*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

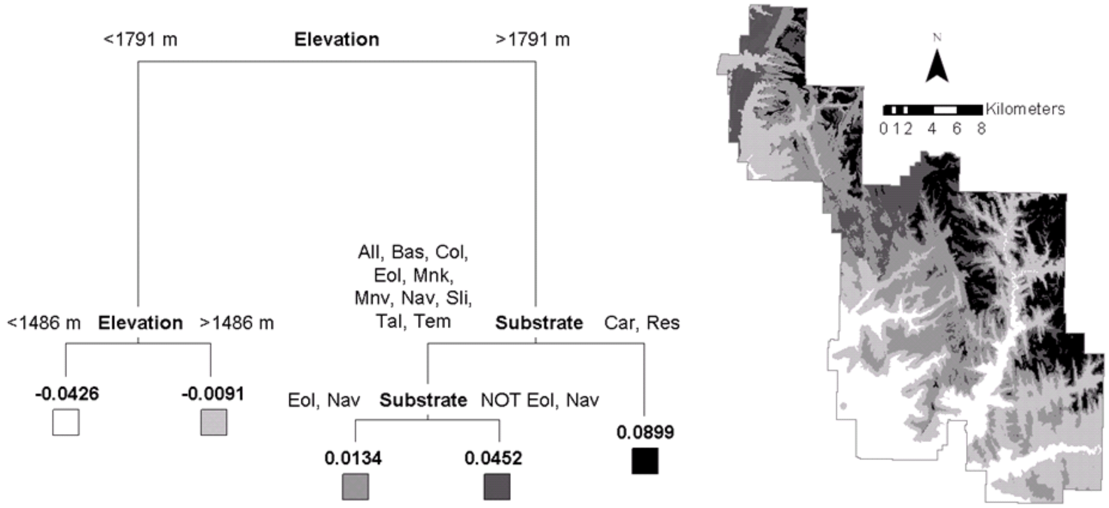


Figure 2.13. Regression tree model and map for the **Mesic Mesa Top** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*Substrate: Car=Carmel, Eol=Eolian, Nav=Navajo, Res=Residuum, see Table 2.1 for translation of other abbreviations*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

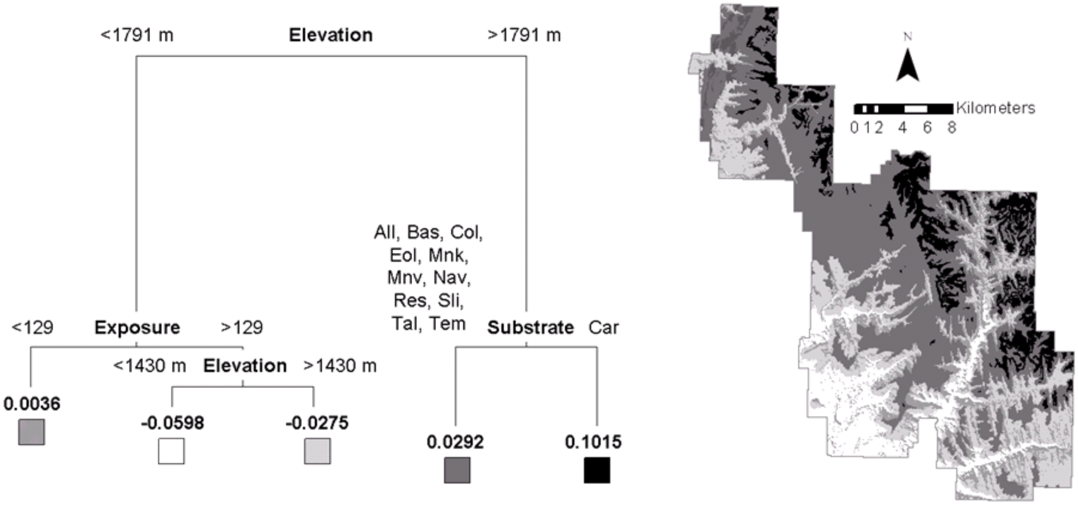


Figure 2.14. Regression tree model and map for the **Xeric Mesa Top** coalition group. Tree model shows relationships between plot affinities and abiotic environmental variables (*Substrate: Car=Carmel, see Table 2.1 for translation of other abbreviations; Exposure=solar hillshade at 215^o azimuth and 45^o altitude*). Mean plot affinity values at terminal nodes are in units of the phi coefficient; higher values (darker shading) = higher affinity. Predicted distribution of affinity values in Zion National Park are mapped using shading shown at tree tips.

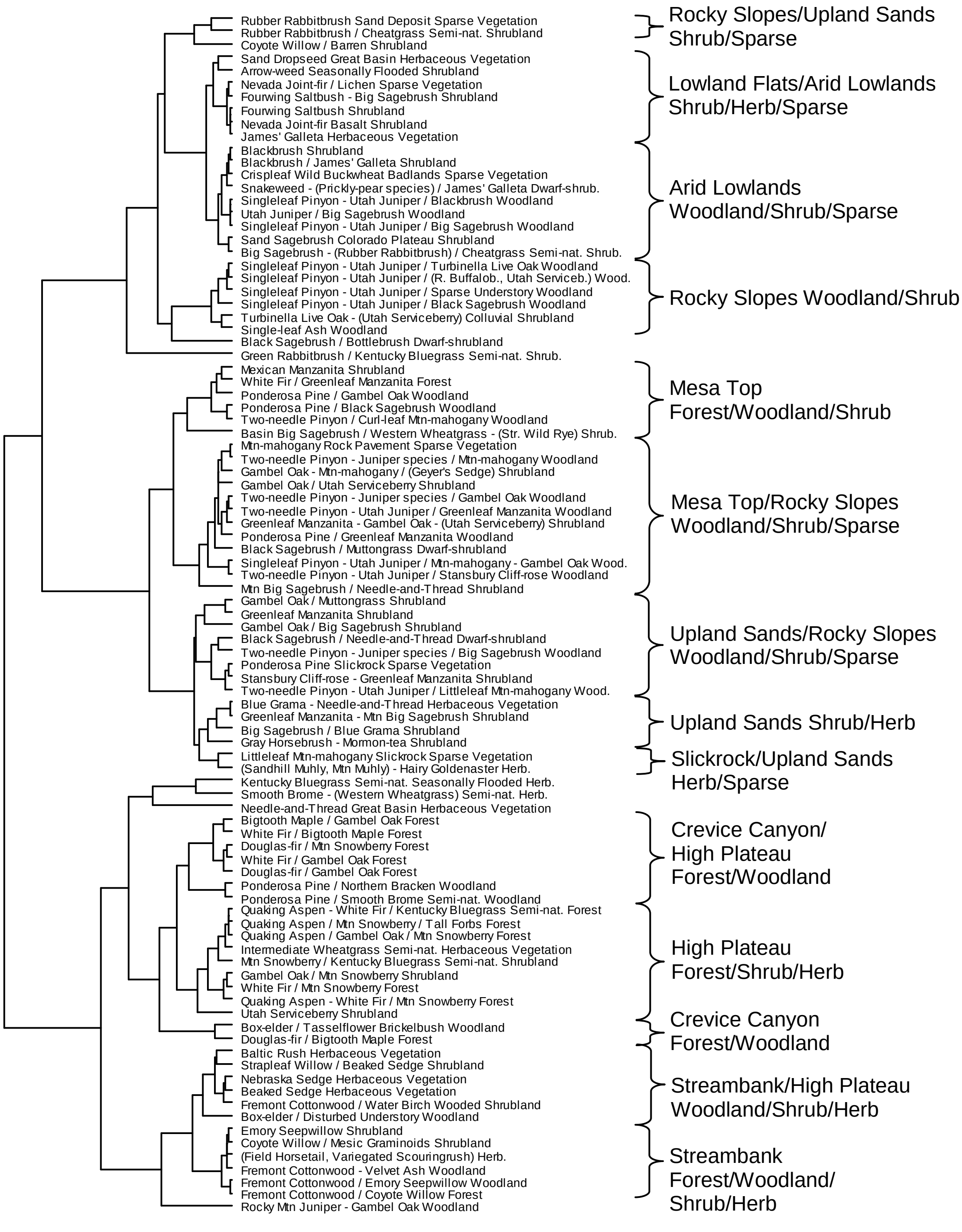


Figure 2.15. Cluster dendrogram of National Vegetation Classification System (NVCS) associations of Zion National Park (Cogan et al. 2004) based on compositional affinities to coalition species groups presented in this paper. Similarities in affinity patterns across species groups were quantified for each NVCS association pair using Pearson's correlation coefficient, then clustered using average linkage hierarchical clustering (McCune and Grace 2002) in R 2.10.1 (R Development Core Team 2010). Names assigned to major clusters (right) combine environmental and physiognomic descriptors.

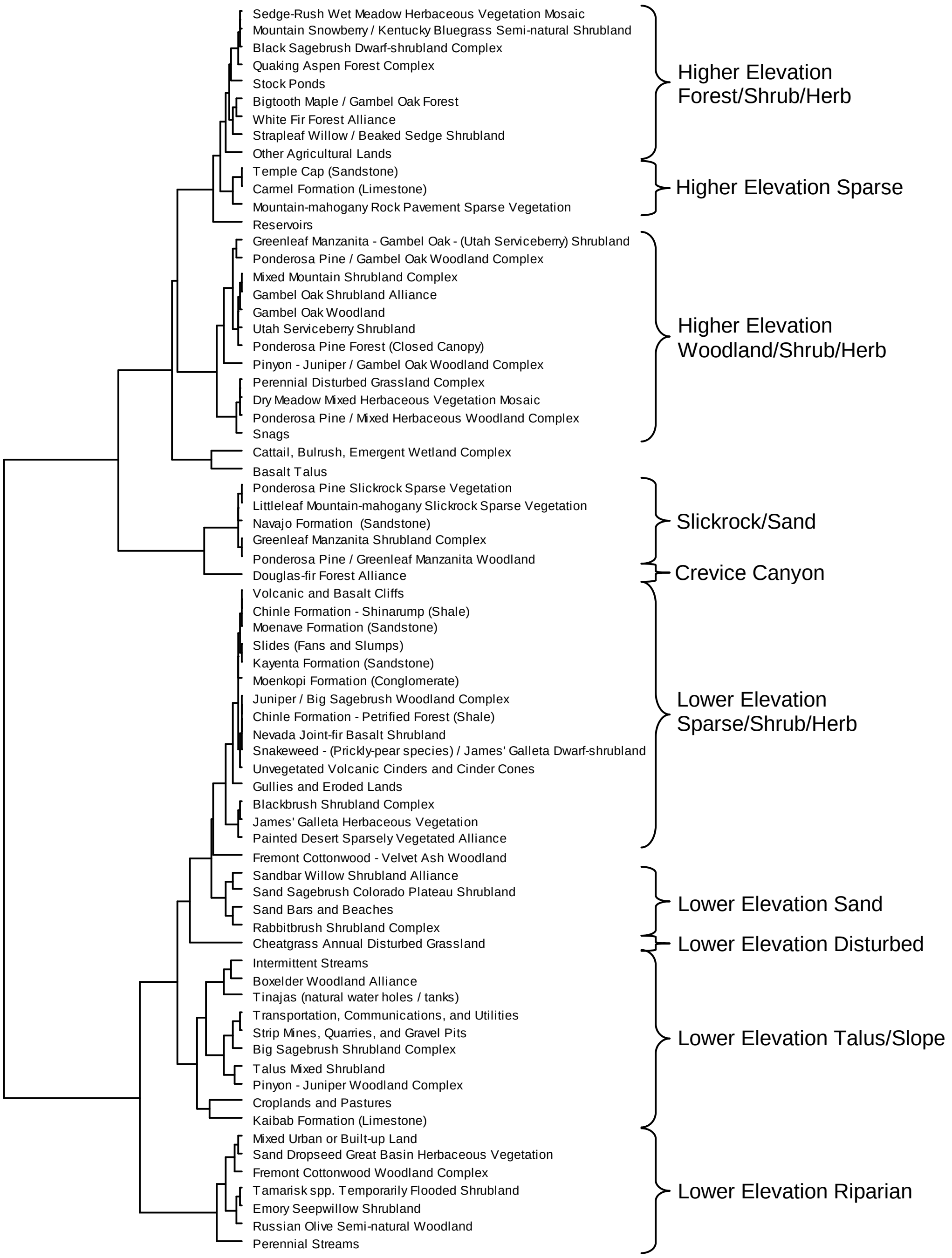


Figure 2.16. Cluster dendrogram of Zion National Park vegetation map units (Cogan et al. 2004) based on pixel-averaged affinities to coalition species groups presented in this paper. Similarities in affinity patterns across species groups were quantified for each map unit pair using Pearson’s correlation coefficient, then clustered using average linkage hierarchical clustering (McCune and Grace 2002) in R 2.10.1(R Development Core Team 2010). Names assigned to major clusters (right) describe their elevational/environmental/ physiognomic characteristics.

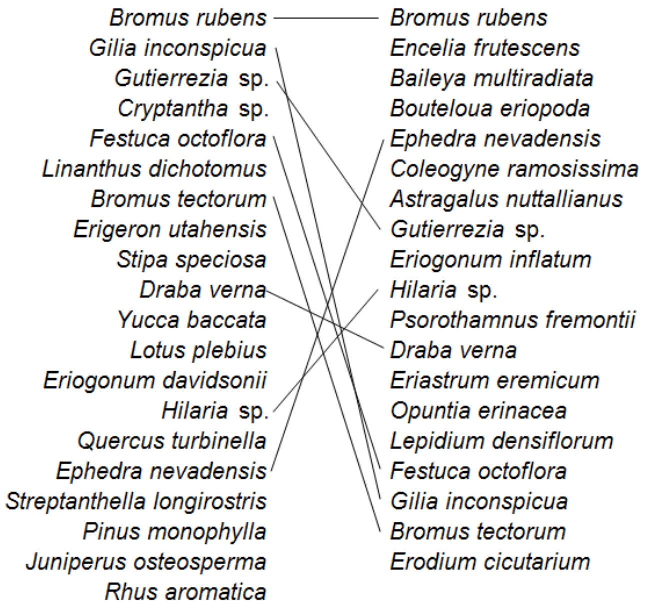


Figure 2.17. Two Arid Lowlands species groups of Zion National Park obtained through coalition clustering in RCLUS at a threshold affinity value of phi=0.2. Species are in descending order of group affinity and lines connect species shared by both groups. The left group has higher elevation/Great Basin affinities and the right group has lower elevation/Mojave Desert affinities.

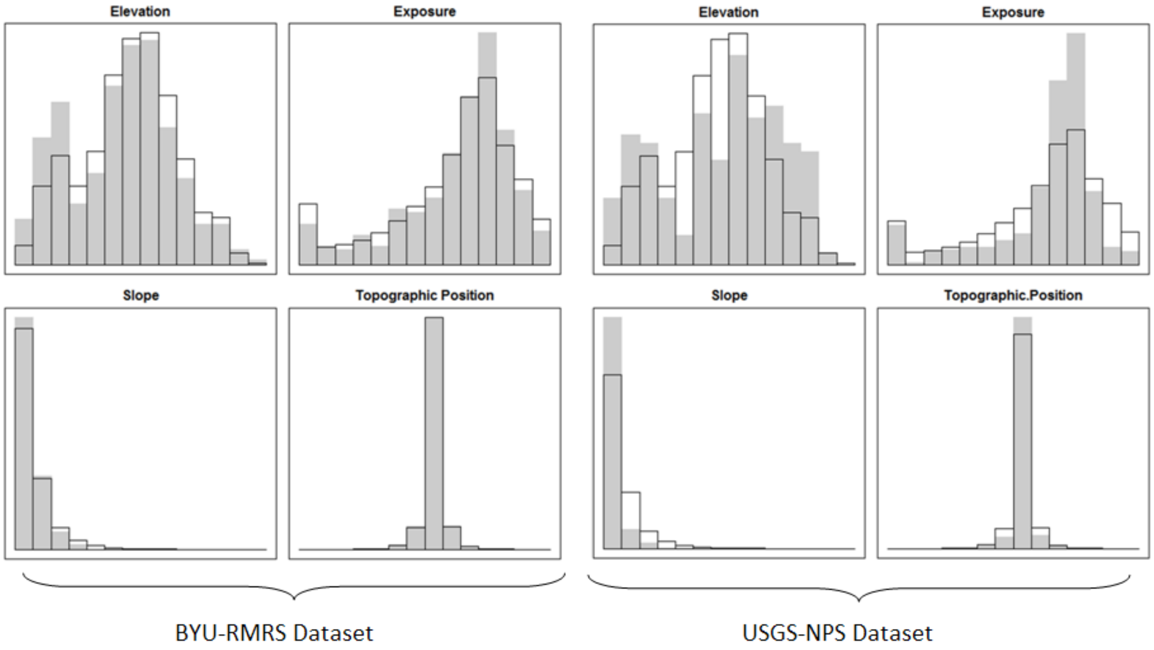


Figure 2.18. Histograms of proportions of background pixels representing four topographic variables at Zion National Park (black line bars) against pixels represented by plots (shaded bars) for the BYU-RMRS dataset (left) and USGS-NPS dataset (right). Based on 50 m pixel resolution generalizations of the original 10 m pixel resolution grids covering the park. Topographic position is TPI at 50 m radius. Created using the adehabitat package (Calenge 2006) in R 2.8.0 (R Development Core Team 2008).

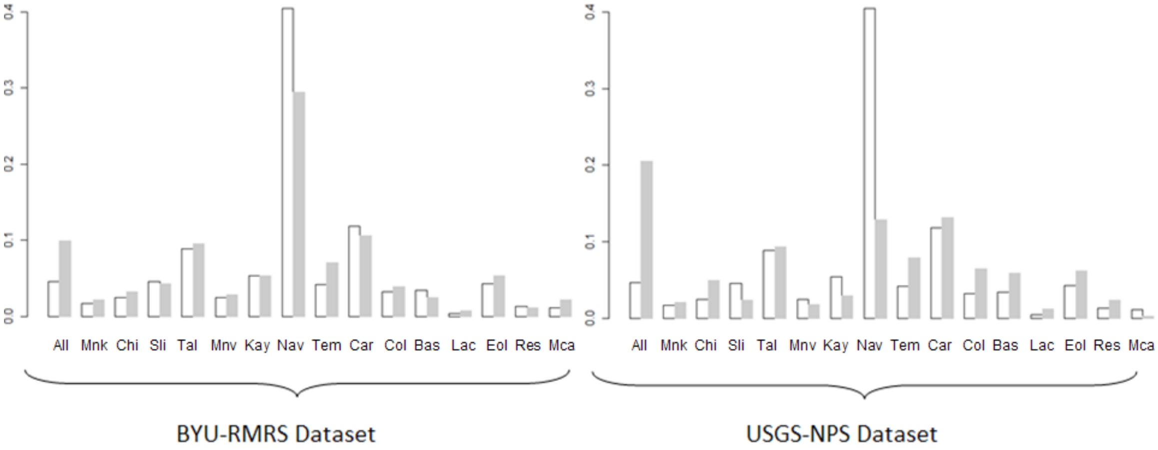


Figure 2.19. Histograms of proportions of background pixels in different geologic substrate classes (see Table 2.1) at Zion National Park (white bars) against pixels represented by plots (shaded bars) for the BYU-RMRS dataset (left) and USGS-NPS dataset (right). Based on 50 m pixel resolution generalizations of the original 10 m pixel resolution grids covering the park. Created using the adehabitat package (Calenge 2006) in R 2.8.0 (R Development Core Team 2008).

Table 2.1. Geologic substrate classes used for environmental modeling of plant species group affinities at Zion National Park. For each substrate class, corresponding map units from a digital geologic map of the Utah Geological Survey (O'Meara 2006) are shown in the rightmost column. Map unit symbols in bold type were represented by one or more plots of the 1987-1989 vegetation survey dataset (Harper 1993).

Code	Substrate Class	Description	Map Units Included in Class
All	Alluvium	river/stream deposits	Qa, **Qa1**, Qa2, **Qac**, Qaco, **Qae**, Qaec, Qaeo, Qaes, Qaf, Qaf1, Qaf2, **Qafc**, Qafco, Qafm, Qafo, Qafy, **Qafy**, **Qage**, **Qal1**, Qaly, **Qam**, Qao, Qao, Qap2, Qas, Qaso, **Qat2**, Qat2, **Qat3**, Qat4, **Qat5**, Qat6, **Qath**, Qatm, Qato, **Qats**, Qav, Qay, Qf
Bas	Basalt	volcanics (flows, cinders, ash)	**Qbc**, **Qbca**, **Qbcc**, **Qbg**, Qbgc, Qbhr, Qblc, **Qblp**, **Qbp**, Qms(b)
Car	Carmel Formation (includes Cedar Mountain Formation)	limestone, shale, sandstone, siltstone, gypsum	**Jccl**, **Jccu**, **Jcp**, Jcw, **Jcx**, Kcmc
Chi	Chinle Formation	mudstone, claystone, siltstone, sandstone, conglomerate	**TRcp**, **TRcp(s)**, **TRcs**
Col	Colluvium	unconsolidated fine gravity deposits	**Qc**, Qce, **Qces**, **Qco**
Eol	Eolian Deposits	unconsolidated wind deposits	**Qea**, **Qed**, **Qer**, **Qes**
Kay	Kayenta Formation	siltstone, sandstone, mudstone	**Jk**, **Jkt**
Lac	Lacustrine Deposits	lake deposits	**Qla**, **Qlbc**, **Qls**
Mca	Mass Movement/ Colluvium/Alluvial Pediment-mantle Deposits	massive gravity deposits mixed with fine gravity deposits and river/stream deposits	**Qmcp1**, **Qmcp2**, **Qmcp3**
Mnk	Moenkopi Formation (includes Kaibab Formation)	siltstone, mudstone, limestone, sandstone, conglomerate, gypsum, dolomite	**TRm**, TRml, TRmm, TRmr, TRms, TRmt, TRmu, **TRmv,** Pkf, Pkh
Mnv	Moenave Formation	mudstone, sandstone, siltstone	**Jm**, Jm(s), **Jmd**, **Jmk(s)**, **Jms**, **Jmw**
Nav	Navajo Sandstone	sandstone	**Jn**, **Jnb**, **Jnl**, **Jnp**, **Jnw**
Res	Residuum	deposits from *in situ* weathering	**Qre**, Qrlc
Sli	Mass Movement (Slide/Slump/Flow) Deposits	massive gravity deposits (slides, slumps and flows)	Qmfy, **Qmsc**, Qmsh, **Qmso**, **Qmsy**
Tal	Talus	coarse gravity deposits	**Qmt**, **Qmts**, **QTng**
Tem	Temple Cap Formation	sandstone, siltstone, mudstone	Jt, **Jts**, **Jtw**

Table 2.2. Coalition species groups and affiliate species of Zion National Park, based on coalition clustering of 1987-89 vegetation survey data. #Occ.=Number of plot occurrences out of a total of 288 plots. Affin.=Affinity of a coalition species to its coalition group, calculated as the mean value of the phi coefficient of association between the species and others in the group. Affil.=Affiliation of an affiliate species with coalition species, in terms of percent co-occurrence. Cvr.=Mean cover of affiliate species weighted by co-occurrences with coalition species (see text for details). Species in boldface are both coalition species and affiliate species for a given group. Underlined species are dominant affiliates (weighted mean cover ≥ 2%)

Coalition Species	**#Occ.**	**Affin.**	**Affiliate Species**	**#Occ.**	**Affil.**	**Cvr.**
Table 2.2A. Streambank						
Baccharis salicina	3	0.4594	***Acer negundo***	18	0.5345	2.34
Salix exigua	3	0.4594	*Bromus tectorum*	130	0.5086	5.10
Tamarix chinensis	5	0.4269	***Bromus diandrus***	10	0.4655	8.28
Populus fremontii	6	0.3936	***Equisetum hyemale***	8	0.4397	0.79
Equisetum hyemale	8	0.3744	*Artemisia ludoviciana*	51	0.4224	0.36
Verbascum thapsus	5	0.3743	***Poa pratensis***	14	0.4224	4.28
***Sonchus* sp.**	3	0.3652	*Poa fendleriana*	190	0.4052	1.78
Agrostis exarata	3	0.3453	*Phacelia heterophylla*	42	0.4052	0.27
Bromus diandrus	10	0.3353	***Elymus trachycaulus***	10	0.3966	0.76
Juncus arcticus	3	0.3103	***Populus fremontii***	6	0.3966	4.63
Elymus canadensis	4	0.2742	*Chrysopsis villosa*	74	0.3879	1.65
Acer negundo	18	0.2513	***Tamarix chinensis***	5	0.3707	0.44
Bromus carinatus	9	0.2511	***Bromus carinatus***	9	0.3621	0.52
Poa compressa	3	0.2434	***Verbascum thapsus***	5	0.3534	0.18
Elymus trachycaulus	10	0.2409	*Quercus gambelii*	135	0.3362	5.75
Poa pratensis	14	0.2027	***Baccharis salicina***	3	0.3017	2.28
Datura wrightii	3	0.2023	***Salix exigua***	3	0.3017	4.98
Fraxinus velutina	6	0.1862	***Elymus canadensis***	4	0.2931	0.15
			Gutierrezia sp.	94	0.2759	0.33
			***Sonchus* sp.**	3	0.2500	0.13
			Agrostis exarata	3	0.2414	0.12
			Fraxinus velutina	6	0.2328	4.19
			Artemisia sp.	2	0.2328	0.44
			Melilotus sp.	2	0.2328	0.12
			Oenothera longissima	2	0.2328	0.12

Coalition Species	#Occ.	Affin.	Affiliate Species	#Occ.	Affil.	Cvr.
Table 2.2B. High Plateau						
Stellaria jamesiana	18	0.3314	*Quercus gambelii*	135	0.8069	22.85
Senecio eremophilus	3	0.3109	***Symphoricarpos oreophilus***	58	0.6455	10.96
Lupinus sericeus	9	0.2937	***Vicia americana***	43	0.6138	5.11
Prunus virginiana	10	0.2923	*Poa fendleriana*	190	0.6081	2.92
Mertensia arizonica	7	0.2907	***Polygonum douglasii***	39	0.4524	0.35
Bromus carinatus	9	0.2714	*Amelanchier utahensis*	141	0.4409	3.08
Amelanchier alnifolia	11	0.2711	*Carex rossii*	67	0.4265	0.44
Stipa nelsonii	5	0.2604	***Stellaria jamesiana***	18	0.4207	2.42
Stipa lettermanii	12	0.2524	*Arabis perennans*	124	0.3487	0.17
Vicia americana	43	0.2497	*Senecio multilobatus*	99	0.3199	0.17
Poa pratensis	14	0.2466	***Juniperus scopulorum***	21	0.3112	0.91
Rosa woodsii	12	0.2403	***Abies concolor***	19	0.3055	3.36
Achillea millefolium	6	0.2048	*Phacelia heterophylla*	42	0.2939	0.19
Taraxacum officinale	11	0.2013	***Poa pratensis***	14	0.2853	4.39
Symphoricarpos oreophilus	58	0.2005	*Eriogonum racemosum*	59	0.2824	0.14
Thalictrum fendleri	12	0.1990	*Solidago velutina*	38	0.2738	1.20
Chenopodium fremontii	3	0.1983	***Prunus virginiana***	10	0.2709	0.72
Abies concolor	19	0.1859	***Stipa lettermanii***	12	0.2651	0.28
Elymus trachycaulus	10	0.1829	***Amelanchier alnifolia***	11	0.2651	0.68
Juniperus scopulorum	21	0.1754	*Acer grandidentatum*	29	0.2622	2.69
Polygonum douglasii	39	0.1711	***Rosa woodsii***	12	0.2594	0.74
Osmorhiza occidentalis	4	0.1617	*Opuntia macrorhiza*	120	0.2565	0.36
Bromus anomalus	5	0.1586	*Pachystima myrsinites*	54	0.2565	1.61
Erigeron speciosus	6	0.1538				

Coalition Species	#Occ.	Affin.	Affiliate Species	#Occ.	Affil.	Cvr.
Table 2.2C. Crevice Canyon						
Eupatorium herbaceum	12	0.3612	*Quercus gambelii*	135	0.6871	7.06
Viola canadensis	5	0.3300	*Poa fendleriana*	190	0.6742	4.52
Cystopteris fragilis	6	0.3184	***Acer grandidentatum***	29	0.6032	6.17
Acer negundo	18	0.3163	***Acer negundo***	18	0.5161	5.54
Polypodium hesperium	6	0.2726	***Eupatorium herbaceum***	12	0.4806	0.24
Galium triflorum	4	0.2616	*Pachystima myrsinites*	54	0.4581	3.26
Acer grandidentatum	29	0.2614	***Pseudotsuga menziesii***	18	0.4548	4.13
Rubus leucodermis	4	0.2611	***Holodiscus dumosus***	21	0.4419	0.87
Bromus ciliatus	12	0.2602	*Solidago velutina*	38	0.4387	0.35
Pseudotsuga menziesii	18	0.2559	***Abies concolor***	19	0.4355	5.46
Heuchera rubescens	12	0.2533	*Draba asprella*	33	0.3903	0.20
Smilacina racemosa	6	0.2531	*Artemisia ludoviciana*	51	0.3871	0.41
Mimulus guttatus	3	0.2451	*Arabis perennans*	124	0.3806	0.19
Taraxacum officinale	11	0.2364	***Heuchera rubescens***	12	0.3806	0.19
Philadelphus microphyllus	10	0.2350	***Bromus ciliatus***	12	0.3774	0.25
Disporum trachycarpum	4	0.2342	*Stephanomeria tenuifolia*	51	0.3742	0.24
Thalictrum fendleri	12	0.2305	***Zauschneria latifolia***	15	0.3710	0.19
Elymus canadensis	4	0.2267	***Selaginella underwoodii***	17	0.3645	0.67
Abies concolor	19	0.2236	*Eriogonum racemosum*	59	0.3613	0.19
Epilobium glandulosum	3	0.2225	*Chrysopsis villosa*	74	0.3452	0.73
Goodyera oblongifolia	5	0.2131	*Senecio multilobatus*	99	0.3323	0.17
Muhlenbergia racemosa	3	0.2055	*Penstemon rostriflorus*	30	0.3323	0.17
Aralia racemosa	3	0.2012	*Mahonia repens*	29	0.3258	0.51
Sphaeromeria ruthiae	3	0.1957	***Thalictrum fendleri***	12	0.3258	0.44
Zauschneria latifolia	15	0.1956	***Philadelphus microphyllus***	10	0.3258	0.69
Holodiscus dumosus	21	0.1947	***Taraxacum officinale***	11	0.2903	0.15
Chimaphila menziesii	5	0.1943	*Phacelia heterophylla*	42	0.2871	0.29
Epilobium ciliatum	3	0.1889				
Epilobium brachycarpum	3	0.1830				
Selaginella underwoodii	17	0.1728				
Brickellia grandiflora	10	0.1723				
Erigeron sionis	4	0.1662				
Aster welshii	6	0.1633				
Pteridium aquilinum	3	0.1626				
Equisetum hyemale	8	0.1603				
Agrostis exarata	3	0.1570				

Table 2.2D. Slickrock

Coalition Species	#Occ.	Affin.	Affiliate Species	#Occ.	Affil.	Cvr.
Petrophytum caespitosum	12	0.3143	*Poa fendleriana*	190	0.8627	4.15
Holodiscus dumosus	21	0.3078	***Chrysopsis villosa***	74	0.6139	1.07
Cercocarpus intricatus	40	0.3022	*Quercus gambelii*	135	0.5574	5.61
Castilleja scabrida	40	0.2903	*Senecio multilobatus*	99	0.5574	0.31
Muhlenbergia thurberi	12	0.2838	*Opuntia macrorhiza*	120	0.5347	0.49
Selaginella underwoodii	17	0.2741	***Pinus ponderosa***	60	0.5347	5.31
Ivesia sabulosa	7	0.2693	***Cercocarpus intricatus***	40	0.5073	1.55
Zauschneria latifolia	15	0.2515	***Stephanomeria tenuifolia***	51	0.5040	0.36
Arenaria fendleri	23	0.2407	***Castilleja scabrida***	40	0.4927	0.25
Erigeron canaani	16	0.2338	*Amelanchier utahensis*	141	0.4863	1.71
Eriogonum jamesii	10	0.2322	*Arabis perennans*	124	0.4766	0.24
Erigeron sionis	4	0.2217	*Arctostaphylos patula*	94	0.4733	5.50
Leptodactylon pungens	8	0.2160	***Arenaria macradenia***	46	0.4087	0.55
Stephanomeria tenuifolia	51	0.2097	*Carex rossii*	67	0.3958	0.28
Draba asprella	33	0.2068	***Solidago velutina***	38	0.3700	0.29
Trifolium longipes	10	0.2031	***Draba asprella***	33	0.3619	0.18
Penstemon humilis	27	0.2021	***Holodiscus dumosus***	21	0.3393	0.58
Pinus ponderosa	60	0.1993	*Eriogonum racemosum*	59	0.3215	0.17
Brickellia grandiflora	10	0.1977	***Penstemon humilis***	27	0.3150	0.23
Chrysopsis villosa	74	0.1966	***Arenaria fendleri***	23	0.3086	0.20
Monardella odoratissima	6	0.1961	*Chaenactis douglasii*	44	0.3053	0.15
Solidago velutina	38	0.1890	*Phlox austromontana*	54	0.2956	0.42
Linanthastrum nuttallii	19	0.1762	*Pachystima myrsinites*	54	0.2827	1.43
Sedum lanceolatum	3	0.1751	***Selaginella underwoodii***	17	0.2811	0.92
Heuchera rubescens	12	0.1744	*Bromus tectorum*	130	0.2682	0.58
Wyethia arizonica	5	0.1696				
Arenaria macradenia	46	0.1502				

Coalition Species	#Occ.	Affin.	Affiliate Species	#Occ.	Affil.	Cvr.
Table 2.2E. Upland Sands						
Cryptantha cinerea	17	0.2622	*Poa fendleriana*	190	0.8255	5.08
Chaenactis douglasii	44	0.2527	***Opuntia macrorhiza***	120	0.7224	1.15
Abronia fragrans	20	0.2521	***Senecio multilobatus***	99	0.6388	0.37
Hymenopappus filifolius	11	0.2352	***Arctostaphylos patula***	94	0.6230	10.05
Artemisia campestris	14	0.2341	*Amelanchier utahensis*	141	0.5515	2.35
Penstemon laevis	26	0.2316	*Quercus gambelii*	135	0.5188	6.57
Tradescantia occidentalis	22	0.2178	***Chrysopsis villosa***	74	0.5006	1.48
Arctostaphylos patula	94	0.2147	*Arabis perennans*	124	0.4800	0.25
Opuntia macrorhiza	120	0.2100	***Erysimum asperum***	64	0.4291	0.21
Eriogonum alatum	6	0.2047	***Pinus ponderosa***	60	0.4085	5.62
Chrysopsis villosa	74	0.1933	***Phlox austromontana***	54	0.4061	0.60
Senecio multilobatus	99	0.1919	*Bromus tectorum*	130	0.3903	1.07
Bouteloua gracilis	19	0.1887	***Chaenactis douglasii***	44	0.3855	0.19
Phlox austromontana	54	0.1886	*Juniperus osteosperma*	115	0.3564	2.21
Arenaria fendleri	23	0.1880	*Gilia inconspicua*	84	0.3406	0.22
Linanthastrum nuttallii	19	0.1760	*Festuca octoflora*	74	0.3345	0.27
Pinus ponderosa	60	0.1735	*Eriogonum racemosum*	59	0.3091	0.16
Erysimum asperum	64	0.1601	*Stephanomeria tenuifolia*	51	0.2970	0.22
Polygonum douglasii	39	0.1548	*Carex rossii*	67	0.2885	0.22
			Polygonum douglasii	39	0.2776	0.14
			Sporobolus cryptandrus	50	0.2703	0.17
			Arenaria macradenia	46	0.2655	0.32
			Yucca angustissima	41	0.2618	0.29
			Stipa hymenoides	65	0.2545	0.17
			Machaeranthera canescens	40	0.2545	0.14
			Penstemon laevis	26	0.2545	0.25

Coalition Species	**#Occ.**	**Affin.**	**Affiliate Species**	**#Occ.**	**Affil.**	**Cvr.**
Table 2.2F. Rocky Slopes						
Fraxinus anomala	45	0.2408	***Poa fendleriana***	190	0.8536	5.78
Arabis perennans	124	0.2379	***Amelanchier utahensis***	141	0.6651	3.47
Erigeron utahensis	41	0.2246	***Arabis perennans***	124	0.6500	0.35
Poa fendleriana	190	0.2132	***Opuntia macrorhiza***	120	0.6126	0.99
Quercus turbinella	50	0.2131	***Juniperus osteosperma***	115	0.5784	4.05
Erysimum asperum	64	0.2064	***Senecio multilobatus***	99	0.5084	0.28
Opuntia macrorhiza	120	0.1969	*Bromus tectorum*	130	0.5004	1.31
Pinus monophylla	64	0.1964	*Quercus gambelii*	135	0.4582	6.98
Juniperus osteosperma	115	0.1868	***Gilia inconspicua***	84	0.4320	0.24
Haplopappus scopulorum	42	0.1804	*Arctostaphylos patula*	94	0.4161	6.24
Shepherdia rotundifolia	17	0.1785	***Erysimum asperum***	64	0.3835	0.19
Penstemon eatonii	23	0.1760	***Pinus monophylla***	64	0.3715	2.94
Amelanchier utahensis	141	0.1661	*Gutierrezia* sp.	94	0.3691	0.52
Senecio multilobatus	99	0.1615	***Quercus turbinella***	50	0.3190	3.64
Gilia inconspicua	84	0.1513	***Fraxinus anomala***	45	0.3047	0.91
Streptanthus cordatus	38	0.1502	*Festuca octoflora*	74	0.2999	0.24
			Cryptantha sp. (annual)	60	0.2872	0.17
			Erigeron utahensis	41	0.2808	0.18
			Stipa hymenoides	65	0.2792	0.22
			Chrysopsis villosa	74	0.2745	0.82
			Eriogonum racemosum	59	0.2673	0.15
			Haplopappus scopulorum	42	0.2673	0.54
			Phlox austromontana	54	0.2649	0.50
			Pinus edulis	53	0.2474	1.84

Coalition Species	#Occ.	Affin.	Affiliate Species	#Occ.	Affil.	Cvr.
Table 2.2G. Arid Lowlands						
Bromus rubens	43	0.3680	***Bromus tectorum***	130	0.7848	3.42
***Gutierrezia* sp.**	94	0.2817	***Gutierrezia* sp.**	94	0.7039	1.26
Baileya multiradiata	8	0.2654	***Juniperus osteosperma***	115	0.6865	4.06
Ephedra nevadensis	18	0.2637	***Gilia inconspicua***	84	0.6424	0.34
Draba verna	40	0.2595	*Poa fendleriana*	190	0.6107	3.16
Gilia inconspicua	84	0.2558	***Festuca octoflora***	74	0.5820	0.43
***Hilaria* sp.**	41	0.2507	*Arabis perennans*	124	0.4908	0.27
Festuca octoflora	74	0.2480	***Cryptantha* sp. (annual)**	60	0.4836	0.27
Coleogyne ramosissima	13	0.2448	***Bromus rubens***	43	0.4826	0.55
Opuntia erinacea	17	0.2280	***Pinus monophylla***	64	0.4518	2.56
Bouteloua eriopoda	5	0.2274	*Opuntia macrorhiza*	120	0.4498	0.73
Eriogonum palmerianum	15	0.2175	***Draba verna***	40	0.3955	0.21
Astragalus nuttallianus	9	0.2167	*Amelanchier utahensis*	141	0.3924	1.97
Bromus tectorum	130	0.2135	***Hilaria* sp.**	41	0.3822	1.10
***Cryptantha* sp. (annual)**	60	0.2085	*Stipa hymenoides*	65	0.3268	0.34
Eriastrum eremicum	7	0.2058	*Quercus turbinella*	50	0.3064	3.53
Psorothamnus fremontii	11	0.2031	*Elymus elymoides*	58	0.3043	0.19
Encelia frutescens	4	0.1980	*Erigeron utahensis*	41	0.2777	0.16
Yucca baccata	17	0.1913	*Arctostaphylos patula*	94	0.2756	4.00
Stipa speciosa	15	0.1855	***Descurainia pinnata***	28	0.2541	0.17
Eriastrum sparsiflorum	13	0.1752	*Artemisia tridentata*	55	0.2377	1.70
Swertia albomarginata	11	0.1751	*Stipa comata*	39	0.2377	1.09
Descurainia pinnata	28	0.1716	*Eriogonum davidsonii*	32	0.2357	0.14
Rhus aromatica	23	0.1709	*Senecio multilobatus*	99	0.2285	0.13
Juniperus osteosperma	115	0.1706				
Eriogonum inflatum	3	0.1657				
Linanthus dichotomus	14	0.1643				
Pinus monophylla	64	0.1617				

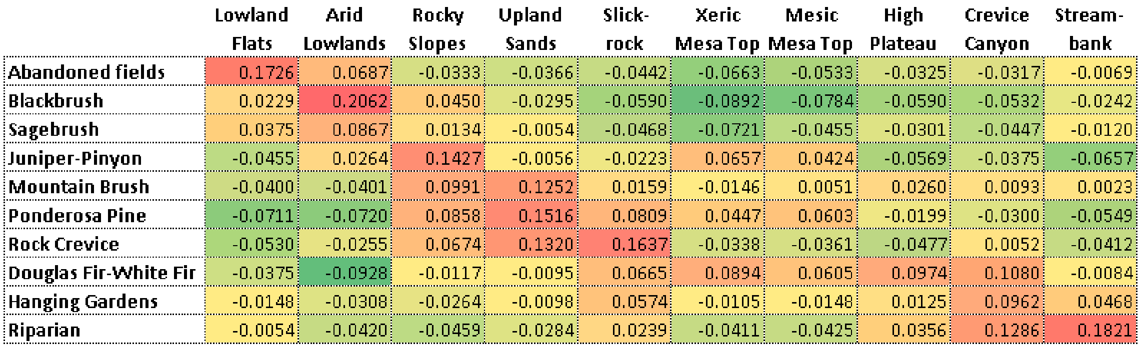
Table 2.2H. Lowland Flats

Coalition Species	**#Occ.**	**Affin.**	**Affiliate Species**	**#Occ.**	**Affil.**	**Cvr.**
Lycium pallidum	3	0.3355	*Bromus tectorum*	130	0.7609	18.04
Erodium cicutarium	10	0.2865	*Gutierrezia* sp.	94	0.5761	1.98
Atriplex canescens	10	0.2722	***Chamaesyce albomarginata***	23	0.5435	1.20
Tragopogon dubius	8	0.2444	*Juniperus osteosperma*	115	0.4783	1.62
Lactuca serriola	13	0.2237	***Sphaeralcea grossulariifolia***	14	0.3913	0.22
Cirsium wheeleri	8	0.2224	***Lactuca serriola***	13	0.3804	0.19
Chamaesyce albomarginata	23	0.2085	***Erodium cicutarium***	10	0.3804	0.82
Sphaeralcea grossulariifolia	14	0.2053	*Hilaria* sp.	41	0.3587	1.30
Elymus smithii	3	0.1929	***Atriplex canescens***	10	0.3478	0.91
			Poa fendleriana	190	0.3152	1.34
			Sporobolus cryptandrus	50	0.3043	0.48
			Festuca octoflora	74	0.2826	0.17
			Stipa comata	39	0.2826	1.41
			Tragopogon dubius	8	0.2826	0.14
			Gilia inconspicua	84	0.2717	0.14
			Amelanchier utahensis	141	0.2609	1.51
			Cirsium wheeleri	8	0.2609	0.18
			Quercus gambelii	135	0.2391	2.61
			Elymus elymoides	58	0.2391	0.15
			Bromus rubens	43	0.2283	0.35
			Cryptantha sp. (annual)	60	0.2174	0.11
			Artemisia tridentata	55	0.2174	1.77

Coalition Species	#Occ.	Affin.	Affiliate Species	#Occ.	Affil.	Cvr.
Table 2.2I. Mesic Mesa Top						
Lathyrus lanszwertii	20	0.2432	***Amelanchier utahensis***	141	0.7787	4.26
Peraphyllum ramosissimum	10	0.2389	***Quercus gambelii***	135	0.7787	15.05
Balsamorhiza sagittata	8	0.2200	*Poa fendleriana*	190	0.7753	4.27
Phlox longifolia	11	0.2187	*Arabis perennans*	124	0.4854	0.25
Penstemon linarioides	13	0.2105	*Opuntia macrorhiza*	120	0.4545	0.78
Swertia radiata	11	0.1982	***Carex rossii***	67	0.4477	0.46
Zigadenus paniculatus	12	0.1945	*Senecio multilobatus*	99	0.4322	0.24
Purshia tridentata	36	0.1832	*Juniperus osteosperma*	115	0.4254	2.51
Quercus gambelii	135	0.1804	***Symphoricarpos oreophilus***	58	0.4099	3.30
Symphoricarpos oreophilus	58	0.1700	***Pinus edulis***	53	0.3911	3.59
Mertensia fusiformis	3	0.1672	*Arctostaphylos patula*	94	0.3774	5.28
Chrysothamnus depressus	5	0.1618	*Pachystima myrsinites*	54	0.3293	1.46
Amelanchier utahensis	141	0.1598	***Purshia tridentata***	36	0.2916	0.71
Carex rossii	67	0.1553	*Pinus ponderosa*	60	0.2813	4.00
Pinus edulis	53	0.1513	*Erysimum asperum*	64	0.2693	0.13
			Bromus tectorum	130	0.2676	0.78
			Vicia americana	43	0.2642	1.55
			Phlox austromontana	54	0.2453	0.69
			Eriogonum racemosum	59	0.2384	0.13
			Cercocarpus montanus	33	0.2316	2.02
			Lathyrus lanszwertii	20	0.2161	0.87
			Solidago velutina	38	0.2041	0.40

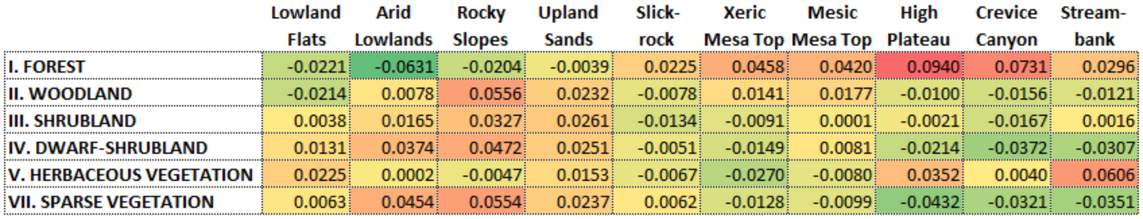
Coalition Species	#Occ.	Affin.	Affiliate Species	#Occ.	Affil.	Cvr.
Table 2.2J. Xeric Mesa Top						
Viola purpurea	10	0.2702	***Amelanchier utahensis***	141	0.7964	4.21
Cercocarpus montanus	33	0.2588	***Quercus gambelii***	135	0.7696	13.94
Pinus edulis	53	0.2160	*Poa fendleriana*	190	0.7464	4.12
Carex rossii	67	0.2114	*Arabis perennans*	124	0.5000	0.25
Pachystima myrsinites	54	0.2096	***Carex rossii***	67	0.4768	0.57
Amelanchier utahensis	141	0.1990	*Opuntia macrorhiza*	120	0.4393	0.79
Swertia radiata	11	0.1911	*Senecio multilobatus*	99	0.4357	0.24
Pedicularis centranthera	10	0.1849	***Pachystima myrsinites***	54	0.4286	1.85
Peraphyllum ramosissimum	10	0.1847	*Arctostaphylos patula*	94	0.4107	5.48
Quercus gambelii	135	0.1792	*Juniperus osteosperma*	115	0.4089	2.65
Physaria newberryi	7	0.1630	***Pinus edulis***	53	0.4089	3.96
Mahonia repens	29	0.1614	*Symphoricarpos oreophilus*	58	0.3250	2.40
			Cercocarpus montanus	33	0.3125	2.91
			Pinus ponderosa	60	0.2732	3.61
			Bromus tectorum	130	0.2500	0.76
			Erysimum asperum	64	0.2464	0.12
			Phlox austromontana	54	0.2375	0.59
			Vicia americana	43	0.2375	1.24
			Mahonia repens	29	0.2357	0.27
			Eriogonum racemosum	59	0.2196	0.12
			Fraxinus anomala	45	0.2196	0.64

Table 2.3. Affinity correspondence between vegetation units of Harper et al. (2001) (rows) and coalition species groups of the current study (columns) at Zion National Park. Low mean phi values (green shading) indicate low correspondence between vegetation types and species groups; high values (red shading) indicate high correspondence.



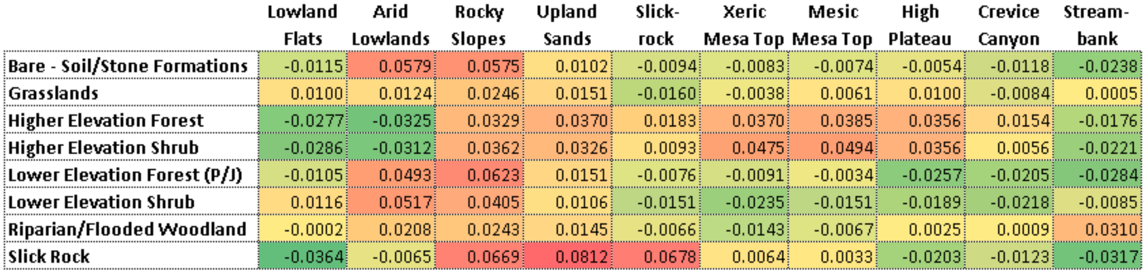
	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slick-rock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Abandoned fields	0.1726	0.0687	-0.0333	-0.0366	-0.0442	-0.0663	-0.0533	-0.0325	-0.0317	-0.0069
Blackbrush	0.0229	0.2062	0.0450	-0.0295	-0.0590	-0.0892	-0.0784	-0.0590	-0.0532	-0.0242
Sagebrush	0.0375	0.0867	0.0134	-0.0054	-0.0468	-0.0721	-0.0455	-0.0301	-0.0447	-0.0120
Juniper-Pinyon	-0.0455	0.0264	0.1427	-0.0056	-0.0223	0.0657	0.0424	-0.0569	-0.0375	-0.0657
Mountain Brush	-0.0400	-0.0401	0.0991	0.1252	0.0159	-0.0146	0.0051	0.0260	0.0093	0.0023
Ponderosa Pine	-0.0711	-0.0720	0.0858	0.1516	0.0809	0.0447	0.0603	-0.0199	-0.0300	-0.0549
Rock Crevice	-0.0530	-0.0255	0.0674	0.1320	0.1637	-0.0338	-0.0361	-0.0477	0.0052	-0.0412
Douglas Fir-White Fir	-0.0375	-0.0928	-0.0117	-0.0095	0.0665	0.0894	0.0605	0.0974	0.1080	-0.0084
Hanging Gardens	-0.0148	-0.0308	-0.0264	-0.0098	0.0574	-0.0105	-0.0148	0.0125	0.0962	0.0468
Riparian	-0.0054	-0.0420	-0.0459	-0.0284	0.0239	-0.0411	-0.0425	0.0356	0.1286	0.1821

Table 2.4. Affinity correspondence between National Vegetation Classification System (NVCS) formation classes of Cogan et al. (2004) (rows) and coalition species groups of the current study (columns) at Zion National Park. Low mean phi values (green shading) indicate low correspondence between formation classes and species groups; high values (red shading) indicate high correspondence.



	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slick-rock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
I. FOREST	-0.0221	-0.0631	-0.0204	-0.0039	0.0225	0.0458	0.0420	0.0940	0.0731	0.0296
II. WOODLAND	-0.0214	0.0078	0.0556	0.0232	-0.0078	0.0141	0.0177	-0.0100	-0.0156	-0.0121
III. SHRUBLAND	0.0038	0.0165	0.0327	0.0261	-0.0134	-0.0091	0.0001	-0.0021	-0.0167	0.0016
IV. DWARF-SHRUBLAND	0.0131	0.0374	0.0472	0.0251	-0.0051	-0.0149	0.0081	-0.0214	-0.0372	-0.0307
V. HERBACEOUS VEGETATION	0.0225	0.0002	-0.0047	0.0153	-0.0067	-0.0270	-0.0080	0.0352	0.0040	0.0606
VII. SPARSE VEGETATION	0.0063	0.0454	0.0554	0.0237	0.0062	-0.0128	-0.0099	-0.0432	-0.0321	-0.0351

Table 2.5. Affinity correspondence between lumped vegetation map units of Cogan et al. (2004) (rows) and coalition species groups of the current study (columns) at Zion National Park. Low mean phi values (green shading) indicate low correspondence between map units and species groups; high values (red shading) indicate high correspondence.



	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slick-rock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Bare - Soil/Stone Formations	-0.0115	0.0579	0.0575	0.0102	-0.0094	-0.0083	-0.0074	-0.0054	-0.0118	-0.0238
Grasslands	0.0100	0.0124	0.0246	0.0151	-0.0160	-0.0038	0.0061	0.0100	-0.0084	0.0005
Higher Elevation Forest	-0.0277	-0.0325	0.0329	0.0370	0.0183	0.0370	0.0385	0.0356	0.0154	-0.0176
Higher Elevation Shrub	-0.0286	-0.0312	0.0362	0.0326	0.0093	0.0475	0.0494	0.0356	0.0056	-0.0221
Lower Elevation Forest (P/J)	-0.0105	0.0493	0.0623	0.0151	-0.0076	-0.0091	-0.0034	-0.0257	-0.0205	-0.0284
Lower Elevation Shrub	0.0116	0.0517	0.0405	0.0106	-0.0151	-0.0235	-0.0151	-0.0189	-0.0218	-0.0085
Riparian/Flooded Woodland	-0.0002	0.0208	0.0243	0.0145	-0.0066	-0.0143	-0.0067	0.0025	0.0009	0.0310
Slick Rock	-0.0364	-0.0065	0.0669	0.0812	0.0678	0.0064	0.0033	-0.0203	-0.0123	-0.0317

CHAPTER 3

PHYLOGENETIC NICHE OVERLAP IN PLANT COMMUNITIES OF ZION NATIONAL PARK

ABSTRACT

Question: Because species sharing common ancestry are likely to have similar niches (phylogenetic niche conservatism), species distributions within and among communities may be non-random with respect to phylogeny. Related species are likely to be segregated at small spatial scales because of alpha niche conservatism, yet aggregated within habitats because of beta niche conservatism. To what extent are these patterns evident across lineages and phylogenetic scales in plant communities?

Location: Zion National Park, Utah, U.S.A.

Methods: **A**lpha- and beta-niche overlap were calculated for all sister groups of a genus-level phylogeny and all congeneric species pairs from a vegetation survey dataset. Alpha-niche was defined at the plot scale, while beta-niche overlap was defined in relation to vegetation classes. A randomization procedure that re-allocated species to plots according to spatial and environmental proximity criteria was used to test statistical significance of each overlap.

Results: Of the 341 congeneric species pairs tested, 42 and 34 showed significant beta-niche aggregation in tests using presence and cover data, respectively. Fewer congeneric species pairs (8 for presence, 7 for cover) showed significant alpha-niche segregation patterns. For sister groups above genus (231 total), an even smaller proportion of tests were significant (8 and 10 for beta niche presence and cover; 1 and 6 for alpha niche presence and cover). A few examples of beta-niche aggregation coupled with alpha-niche aggregation were noted but none were simultaneously significant for both. On the other hand, other patterns suggesting various types of niche divergence were common. Many related taxa were segregated in their beta as well as alpha-niche, suggesting divergence of habitat affinities driven by competitive interactions. Others were aggregated in both niche types, suggesting evolution of coexistence mechanisms.

Conclusions: These results draw attention to the complex mixture of niche conservatism and divergence in plant lineages and demonstrate that niche conservatism cannot be uncritically invoked in community assembly studies.

INTRODUCTION

Studies addressing phylogenetic patterns in ecological communities have the potential to provide greater insight than those based simply on species patterns (Webb et al. 2002, Webb et al. 2006, Emerson and Gillespie 2008, Cavender-Bares et al. 2009, Vamosi et al. 2009). Because ecological traits have an evolutionary origin, and may be preserved over evolutionary time through phylogenetic niche conservatism (Harvey and Pagel 1991), species sharing common ancestry may assemble themselves into communities in predictable ways. In an influential review paper, Webb et al. (2002) described two potential consequences of phylogenetic niche conservatism on community structure: (1) phylogenetically-related species are likely to be segregated (spatially overdispersed) at small spatial scales corresponding to local neighborhoods of interacting individuals because conserved niche similarity should result in competitive exclusion;

although (2) at larger spatial scales encompassing habitat variation, related species are likely to be aggregated (spatially clustered) due to conserved similarities in their habitat affinities (Webb et al. 2002; see also Cavender-Bares et al. 2009, Vamosi et al. 2009). By consolidating these predictions into an explicitly phylogenetic model and offering analytical tools for measuring phylogenetic relatedness of entire communities, Webb et al. (2002) set in motion a subdiscipline of ‘community phylogenetics’ (Swenson et al. 2006) intent on testing for phylogenetic segregation and aggregation through empirical analysis of field data (Webb et al 2006, Cavender-Bares et al 2009, Vamosi et al. 2009).

Terrestrial plant communities have been particularly well represented in phylogenetic community studies, apparently in part because of their stationary spatial structure and ease of sampling (Vamosi et al. 2009). The sample units of plant community studies (vegetation plots) are typically spatially defined areas within which plant species composition and abundance can be exhaustively inventoried at a given point in time. Appropriately-sized vegetation plots can be construed as local neighborhoods of interacting plant species. Whittaker (1975) used the term *alpha diversity* to refer to species diversity at local scales exemplified by plots, and by extension the term *alpha niche* has been used to describe niche characteristics permitting (or not) local species coexistence (Pickett and Bazazz 1978, Silvertown et al. 2006). The *beta niche*, like *beta diversity*, refers to a broader scale of environmental differentiation, i.e. the scale of multiple plots arranged along an environmental gradient. Moisture requirements and edaphic preferences are examples of beta niche attributes, while resource acquisition strategy fits the alpha niche category (Silvertown 2004, Silvertown et al. 2006). The alpha niche translates to those aspects of the niche that Webb et al. (2002) predicted would lead to local segregation of phylogenetically-related species, and the beta niche translates to habitat affinities that should lead to phylogenetic aggregation by habitat.

Empirical analyses of phylogenetic structure in plant communities have revealed instances of phylogenetic segregation and aggregation consistent with the alpha/beta-niche conservatism model (reviewed in Cavander-Bares et al. 2009, Vamosi et al. 2009). However, different phylogenetic structure patterns have been noted for different lineages, locations, and scales. Several authors have pointed out that taxonomic or phylogenetic scale (the number of lineages under consideration) affects the outcome of phylogenetic community analyses (Slingsby and Verboom 2006, Cavander-Bares et al. 2006, Swenson et al. 2006, 2007). Cavender-Bares et al. (2006), for example, observed alpha-scale phylogenetic segregation within certain narrowly-defined lineages (e.g. the genus *Quercus*, see also Cavender-Bares et al. 2004), but phylogenetic aggregation when all seed plants were considered simultaneously. These results suggest that the strength and/or effects of niche conservatism vary across lineages having different degrees of shared evolutionary history. One might expect the imprint of niche conservatism to be more pronounced within a narrow, recently-evolved lineage than a broad, ancient lineage that has had more time to diverge ecologically (Vamosi et al. 2009). But because different lineages have the potential to evolve at different rates and in different ways, the balance between niche conservatism and divergence may not be consistently related to lineage age (or other measures of phylogenetic relatedness). Given these considerations, phylogenetic community structure may not be as easily predicted as the alpha-beta niche conservatism model implies. Rather than asking whether phylogenetic aggregation or segregation is detectable in a community as a whole, one may need to dissect the community to discover the specific lineages, scales and circumstances under which such patterns are evident.

This paper presents an analysis of phylogenetic community structure using data from Zion National Park, Utah, U.S.A. (Cogan et al. 2004). One of my objectives is simply to add an evolutionary dimension to previous species-based plant community characterizations of the park. I also wish to add to the body of studies that have examined phylogenetic community structure in other settings. However, unlike many previous studies my objective is not to quantify general patterns of phylogenetic structure using lineage age or other phylogenetic relatedness measures. Instead, I aim to document the extent to which patterns of aggregation and segregation can be found across different lineages and phylogenetic scales. I adopt a comprehensive exploratory approach examining patterns individually for each lineage and node of a community phylogeny. With this approach, phylogenetic relatedness (branch length) information is not required and community phylogenetic structure is re-cast as niche overlap between sister groups (cf. Warren et al. 2008). I explore niche overlap based on abundance (measured as cover) as well as presence/absence.

METHODS

Study Area and Plant Community Data

Zion National Park (Zion) is world-renowned for its geologic formations, including its massive colored sandstone cliffs, towers and canyons. Zion is also ecologically significant because of its environmental heterogeneity and high biological diversity. Numerous floristic studies and plant community/vegetation studies (e.g., Woodbury 1932, Meyer 1974, Welsh 1989, Harper 1993, Cogan et al. 2004, Fertig and Alexander 2009) have documented the geography and ecology of plants within the park. The current study builds on a vegetation survey carried out at Zion in 1999-2000 as part of the U.S. Geological Survey (USGS)-National Park Service (NPS) Vegetation Characterization and Mapping Program (Cogan et al. 2004).

The USGS-NPS vegetation survey at Zion utilized a gradsect strategy (Gillison and Brewer 1985) to stratify the park's environment into zones differentiated by elevation, substrate, hydrology, solar insolation and fire history (Cogan et al. 2004). Gradsect zones provided sampling targets for vegetation survey crews who ultimately placed plots at sites considered homogeneous and representative of major vegetation types. Plot size varied with vegetation type: 100 m^2 for vegetation dominated by herbs or dwarf shrubs, 400 m^2 for shrub- and tree-dominated vegetation. In some areas, e.g. narrow riparian zones, plots took a rectangular shape; otherwise plots were square or circular (Cogan et al. 2004). A Daubenmire (1959) cover class (or in some cases, a direct percent cover estimate) was recorded by species and vegetation stratum for vascular plant species occurring within plots. Eight vegetation strata were used: herbs, vines, three shrub size classes, and three tree size classes (Cogan et al. 2004). Additional species occurring near but not within plot boundaries were listed for some plots, but cover was not recorded for these species.

Cogan et al. (2004) used the USGS-NPS plot data to classify and map the vegetation of Zion following the U.S. National Vegetation Classification System (NVCS) (Grossman et al. 1998, Jennings et al. 2009). Multivariate analyses of species cover data in PC-ORD (McCune and Mefford 1997) guided the classification process (Cogan et al.

2004). At the time of data release in 2004, 332 of the 346 plots had been formally classified to the association and alliance levels of the NVCS (Cogan et al. 2004, USGS 2004). I grouped alliances into ten 'ecological divisions' (Table 3.1) that reflect major environmental settings at Zion, modified from ecological groupings imbedded in the digital vegetation map accompanying the vegetation classification (Cogan et al. 2004, USGS 2004). I used the combination of ecological divisions, alliances and associations to define habitat or beta-niche variation for testing phylogenetic niche overlap.

Taxonomic/phylogenetic Data Synthesis

Vascular plant species recorded by the USGS-NPS vegetation survey (Cogan et al. 2004), following Kartesz (1999), were standardized to the nomenclature of Welsh et al. (2003) for consistency with accepted usage by the U.S. National Park Service at Zion (Fertig and Alexander 2009) (Appendix 3.1). However, classification at the genus level and above followed the National Center for Biotechnology Information (NCBI 2008), which in some cases differed from Welsh et al. (2003) in name and/or circumscription (e.g. spitting of the genus *Aster*) (Appendix 3.1). The NCBI (2008) taxonomic classification provided a working hypothesis of phylogenetic relationships that was refined and modified where appropriate to match recent findings of plant systematists (Table 3.2). For angiosperms, ordinal phylogenetic relationships were based on APG III (APG 2009) and relationships of families within orders were obtained from Davis et al. 2004 (monocots), Tank et al. 2006 (Scrophulariaceae s.l.), Stevens 2008 (angiosperms in general) and Wang et al. 2009 (Ranunculales). Fern family relationships were obtained from Smith et al. (2006) and Schuettpelz and Pryer (2007). Nearly all polychotomies in a genus-level phylogenetic supertree (Fig. 3.1) could be resolved using this approach[1]. Although I made no attempt to integrate branch length information into the phylogeny, I use taxonomic ranks as benchmarks of phylogenetic depth relative to the genus level.

Niche Overlap Calculations

Using species occurrence and cover data from the 332 classified USGS-NPS vegetation plots, combined with taxonomic/phylogenetic information for each species, I calculated niche overlap for all ‘sister’ group pairs for each dataset. The number of ‘sister’ groups was expanded to include all species pairs within genera (Appendix 3.2) as well as pairs at phylogenetic nodes above the genus level (Appendix 3.3, Fig. 3.1).

Niche overlap was calculated using the Renkonen index (Krebs 1999) which measures the overlapping area under two discretely-defined niche occupancy curves:

$$\mathrm{P}_{\mathrm{jk}} = \sum_{i=1}^{n} \left(\min p_{ij}, p_{ik}\right)$$

where P_{jk} = Renkonen index between group i and group j (as a proportion)
p_{ij} = Proportion niche state i is of the total niche of group j
p_{ik} = Proportion niche state i is of the total niche of group k
n = Total number of niche states

As used here, ‘groups’ are congeners or sister groups and ‘niche states’ are spatial units representing variation of alpha and beta niches. For alpha niche overlap calculations, each vegetation plot was a single niche state. For beta niche calculations, niche states were defined by vegetation classes. Plots belonging to the same association were

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[1] Available literature was insufficient to resolve ordinal relationships within the core lamiids (Gentianales, Lamiales/Solanales and Boraginaceae) and familial relationships within the Malpighiales (Euphorbiaceae, Linaceae, Salicaceae, and Violaceae). For the analysis presented here these groups were arbitrarily nested as (Gentianales, (Lamiales/Solanales, Boraginaceae)) and ((Euphorbiaceae, Linaceae), (Salicaceae, Violaceae))

considered to be identical beta niche units, whereas plots belonging to the same alliance but different associations were considered 2/3 similar, plots belonging to the same ecological division but different alliances were 1/3 similar, and plots belonging to different ecological divisions had a beta niche similarity of zero.

All niche overlap calculations were carried out twice, once for presence/absence (i.e. co-occurrence) and once for cover, using arithmetic midpoints of cover classes as percent cover values. Cover calculations posed an interesting challenge in that cover values of individual species and strata had to be aggregated at multiple levels. Cover values were first aggregated across strata for each species, then across species for each higher phylogenetic grouping. Because of overlapping cover within plots, simple summation of cover values was not satisfactory, leading to aggregated cover values in excess of 100%. This problem was overcome through a sequential, probabilistic algorithm as illustrated in Fig. 3.2. Cover values to be aggregated were sorted from highest to lowest and accreted in sequence. The question of how much additional cover to add with each additional species was resolved by assuming (given the absence of further information) that cover was proportionally distributed between overlapping and non-overlapping portions. Thus a species with 35% cover would contribute an additional 14% (0.35*0.40) to an existing total of 60% since the other 21% (0.35*0.60) is assumed to overlap with the existing total (Fig. 3.2).

Significance tests

The statistic of interest in this analysis was not niche overlap *per se* but the degree to which overlap was greater than expected (aggregation) or less than expected (segregation) relative to null models. Using the R package for statistical computing (R Development Core Team 2009) I generated null distributions of alpha and beta niche overlap against which observed overlap values were compared. Plot occurrences (and corresponding cover values) were randomized 1000 times for each congeneric pair and sister group comparison. This procedure resembles niche overlap randomization tests in the EcoSim program (Gotelli and Entsminger 2009) except that I added spatial criteria to the randomization process. Re-allocation probabilities were not truly random but rather proportional to distance, such that an occurrence was more likely to be re-allocated to a plot in close proximity (including the plot where actually observed). In this way, dispersal effects were incorporated into null models and randomization tests were conservative with respect to pseudoreplication risks (cf. Wilson 2007).

For alpha niche overlap tests I imposed additional constraints on the randomization process to ensure that I was testing for overlap within rather than between habitats. I multiplied re-allocation probabilities based on spatial proximity by probabilities based on habitat similarity. Following the same scale used in niche overlap calculations (previous section), a similarity value of 3 was given to plots within the same association, 2 for plots in different associations of the same alliance, 1 for plots in different alliances of the same ecological division, and 0 for plots in different ecological divisions. Consequently, occurrences were never re-assigned to a different ecological division when testing alpha niche overlap, and were more likely to be re-assigned within their own alliance and association.

RESULTS AND DISCUSSION

Although the repetitive significance testing approach followed here does not adhere to strict statistical standards, it poses little problem in an exploratory framework (cf. Tukey 1980). As noted in my methods description, I expanded the exploratory realm to include comparisons of all possible congeneric species pairs. This was partially a practical move, since well-resolved phylogenies integrating all species of interest were unavailable for many plant genera at Zion. It also represents an attempt to look beyond the strict confines of bifurcating phylogenetic models. Since hybridization and introgression are known to occur among closely-related species in many plant groups (Stebbins 1969, Linder and Rieseberg 2004, Whitney et al. 2010), reticulate evolutionary models may in many cases be more accurate representations of intra-generic relationships than phylogenetic trees. Diffuse comparisons among all congeneric species pairs leave this possibility open for examination.

Niche overlap test results for congeneric species pairs (Table 3.3A, Appendix 3.2) and phylogenetic sister groups (Table 3.3B, Fig. 3.3-3.6, Appendix 3.3) are given as probabilities ranging from -1 to 1. Probability values above and below zero indicate greater aggregation and segregation, respectively, than expected relative to null models, and values above 0.95 and below -0.95 correspond to $p<0.05$ in a two-tailed significance test. Only a portion of tests were statistically significant and many did not even deviate from the null expectation (Table 3.3). Alpha niche overlap tests, in particular, had a high number of null results, suggesting that these tests were particularly conservative and/or had low statistical power. The number of plots available for randomization was low for some habitats within which alpha niche overlap randomizations were constrained. In addition, both alpha and beta niche overlap tests had low power among species or groups with few occurrences. An increase in the proportion of significant test results can be seen when moving from species, some of which occurred only once in the dataset, to higher taxonomic levels where species aggregation resulted in larger sample sizes (Fig. 3.3-3.6, Appendices 3.2-3.3).

In accordance with the alpha-beta niche conservatism model, I expected beta niche overlap tests to yield numerous cases of aggregation by habitat, and segregation by plot within habitats for alpha niche overlap tests. I was especially interested in finding examples of beta niche aggregation coupled with alpha niche segregation. Several species pairs and sister groups fit this coupled pattern, including *Echinocereus engelmannii/E. triglochidiatus*, *Opuntia basilaris/O. macrorhiza*, *Phlox austromontana/P. hoodii*, *Purshia mexicana/P. tridentata*, *Gutierrezia microcephala/G. sarothrae*, *Arabis/Draba*, and Boraginoideae/Hydrophylloideae. However, these cases were limited and none of them were simultaneously statistically significant for both beta niche aggregation and alpha niche segregation, whether measured using presence or cover.

On the other hand, many tests revealed patterns different from the expectations of the alpha-beta niche conservatism model. Some pairs were segregated by plot within habitats, suggesting alpha niche conservatism, but were also more segregated than expected among habitats, suggesting beta niche divergence. These may be examples of taxa that have a history of competition with one another, leading to the evolution of different habitat affinities that reduce competitive encounters—Connell's (1980) "ghost of competition past". Many of the taxon pairs that fit this pattern are dominants that may indeed be in competition with one another, e.g. the trees *Pinus edulis/P. ponderosa*; shrubs *Quercus gambelii/Q. turbinella*, and *Amelanchier alnifolia/A. utahensis*; grasses *Poa fendleriana/P. pratensis*; and even higher taxa such as commelinids/misc. monocots, Ericales/[lamiids + campanulids] and Gymnosperms/Magnoliophyta. In many of these cases, alpha niche segregation was more significant when measured using cover, which would be expected to be a more sensitive measure of competitive effect than presence/absence.

The opposite pattern, aggregation by both habitat and plot, was also fairly common and significant. This pattern suggests beta niche conservatism combined with alpha niche divergence, i.e. related taxa with similar habitat affinities that appear to have evolved coexistence mechanisms. Taxa with riparian/wetland affinities are especially well represented in this group, including Cyperaceae/Juncaceae, *Populus/Salix* and various species pairs within *Juncus*. At the opposite moisture extreme, several members of the cactus genus *Opuntia* also fall in this category.

The most surprising and puzzling result was the widespread coupling of significant beta niche segregation with alpha niche aggregation. Many sister groups overlapped less often than expected in their habitat preferences, but when they did occur in the same habitat they tended to also occur in the same plot. This pattern suggests the ability to coexist due to alpha niche divergence, but why this would lead to increased co-occurrence despite different habitat preferences is difficult to explain. One possibility is that these groups are responding to environmental variation that was not captured by vegetation-based habitat characterizations. Groups exhibiting this pattern spanned a range of lineages and scales, e.g. *Elymus elymoides/E. lanceolatus*, *Acer* *grandidentatum/A. negundo*, *Bromus diandrus/B. tectorum*, *Echinocereus/Opuntia*, Anthemideae/Astereae, Cupressaceae/Pinaceae, and fabids/malvids.

CONCLUSIONS

Despite the limitations of the USGS-NPS plant community dataset, the exploratory null model approach used in this study proved useful for quantifying alpha and beta niche overlap across multiple lineages and phylogenetic scales at Zion. Predicted patterns of beta niche aggregation and alpha niche segregation were detected for some lineages and scales but were countered by numerous instances of other patterns suggesting niche divergence rather than conservatism. These results suggest that phylogenetic niche conservatism has left an imprint on plant community patterns at Zion, but only to a limited extent. Mirroring the criticisms of Giannani (2003) and Losos (2008), who questioned that assumption that phylogenetic relatedness and ecological similarity are consistently correlated, this study raises questions regarding the universality of the alpha-beta niche conservatism community assembly model.

Results of this study are best viewed as preliminary since they could be followed up with additional exploratory analyses as well as other research approaches. A larger vegetation plot sample is needed to fully characterize plant community patterns at Zion, including the many plant species known to occur in the park that were not represented in the USGS-NPS dataset (Cogan et al. 2004, Fertig and Alexander 2009). The discrete, vegetation-based habitat classes used in this study may not be the optimal way to characterize environmental variation at Zion; continuous-scale environmental models (e.g. regression tree models introduced in Chapter 2) offer an alternative. The spatial scale of the current analysis may also be suboptimal for detecting phylogenetic community patterns. A smaller spatial grain (plot size) than 100-400 m^2 might be necessary to accurately capture the ‘neighborhood’ zone of alpha niche interactions, especially for species that are small in stature. A larger spatial extent (study area size), covering the entire region surrounding Zion or beyond, might reveal additional cases of beta niche conservatism if it captures allopatric relatives of species occurring at Zion (see Chapter 4).

Empirical analyses of community phylogenetic structure are but a starting point for understanding the influence of evolutionary history on community assembly. Phylogenetic aggregation and segregation patterns suggest but do not confirm phylogenetic niche conservatism. More explicit studies are needed to experimentally demonstrate the effects of competition and habitat filtering, and to identify specific, phylogenetically-conserved traits related to the alpha and beta niche. The study presented here highlights putative cases of phylogenetic niche conservatism that may be worth investigating in greater detail.

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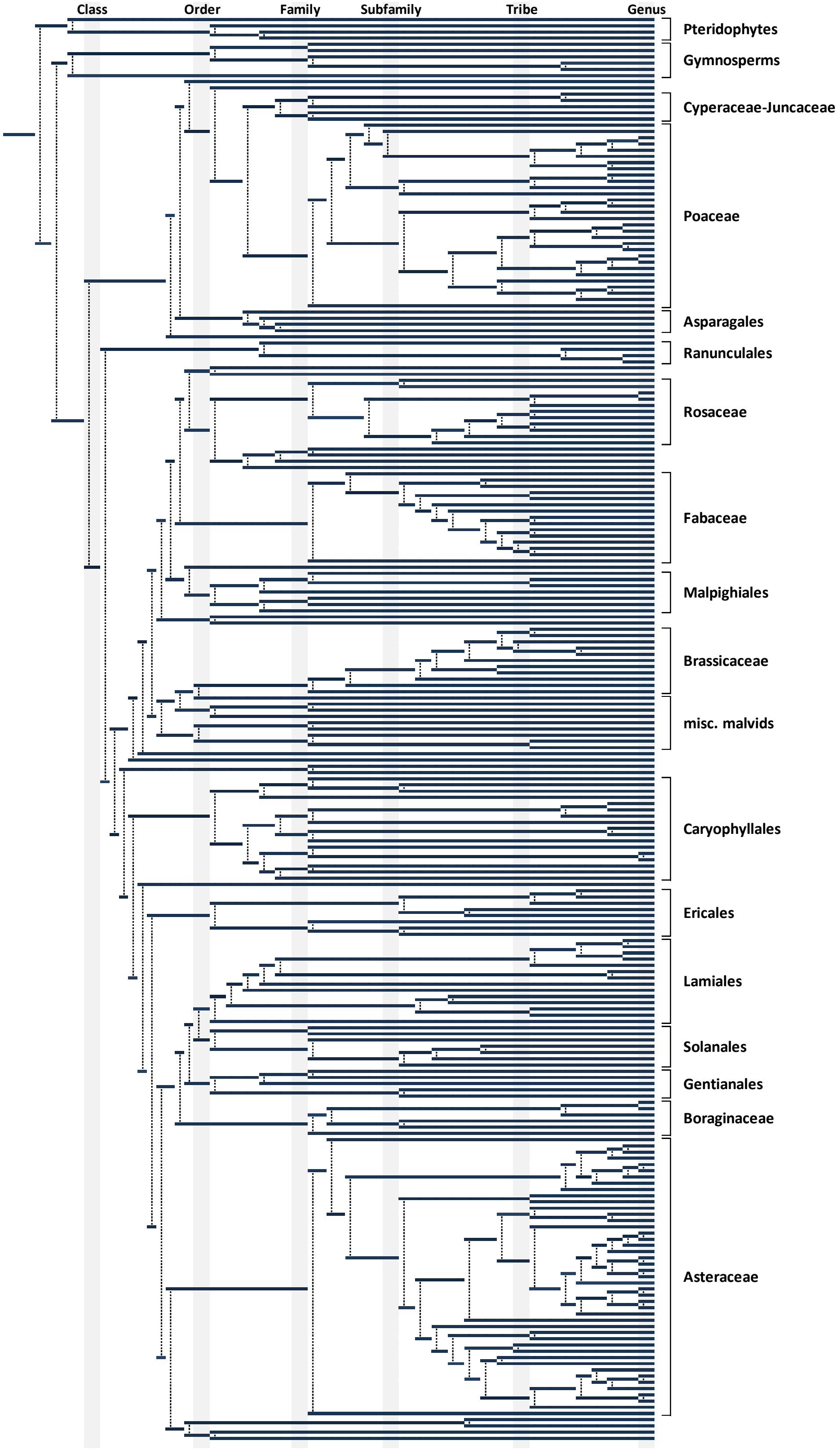

Figure 3.1. Genus-level phylogenetic supertree of vascular plants reported in the USGS-NPS vegetation survey of Zion National Park (Cogan et al. 2004).

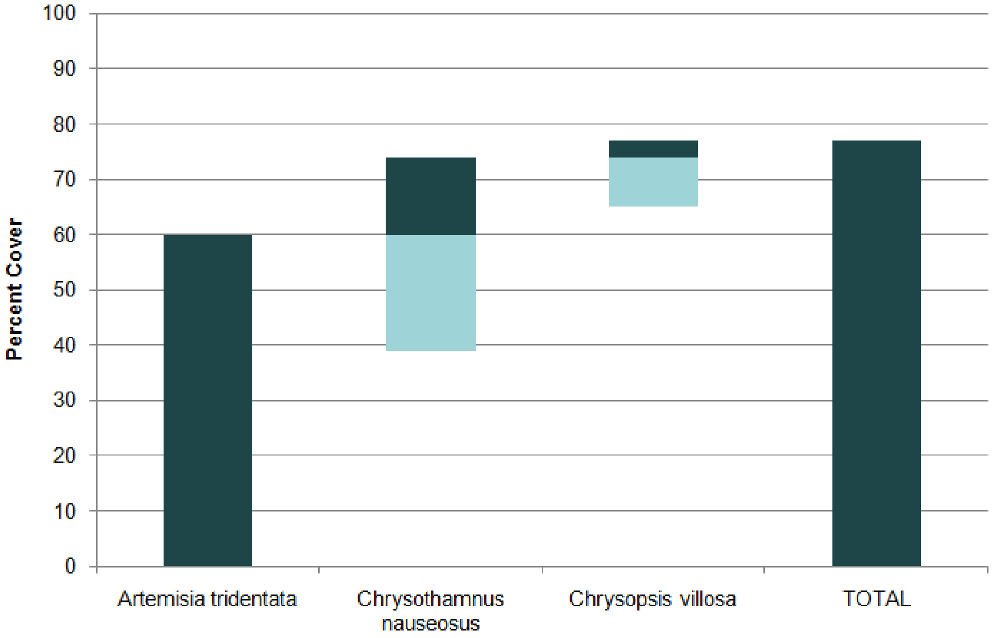

Figure 3.2. Hypothetical scenario illustrating procedure for aggregating cover values of multiple species (or strata) within plots. Three species are arranged in descending order of cover (*Artemisia tridentata*, 60%; *Chrysothamnus nauseosus*, 35%; *Chrysopsis villosa*, 12%). Building on total cover of the first species, cover of secondary species is added as a proportion (dark) of their total cover (dark + light blue) equivalent to the proportion of the plot not yet covered.

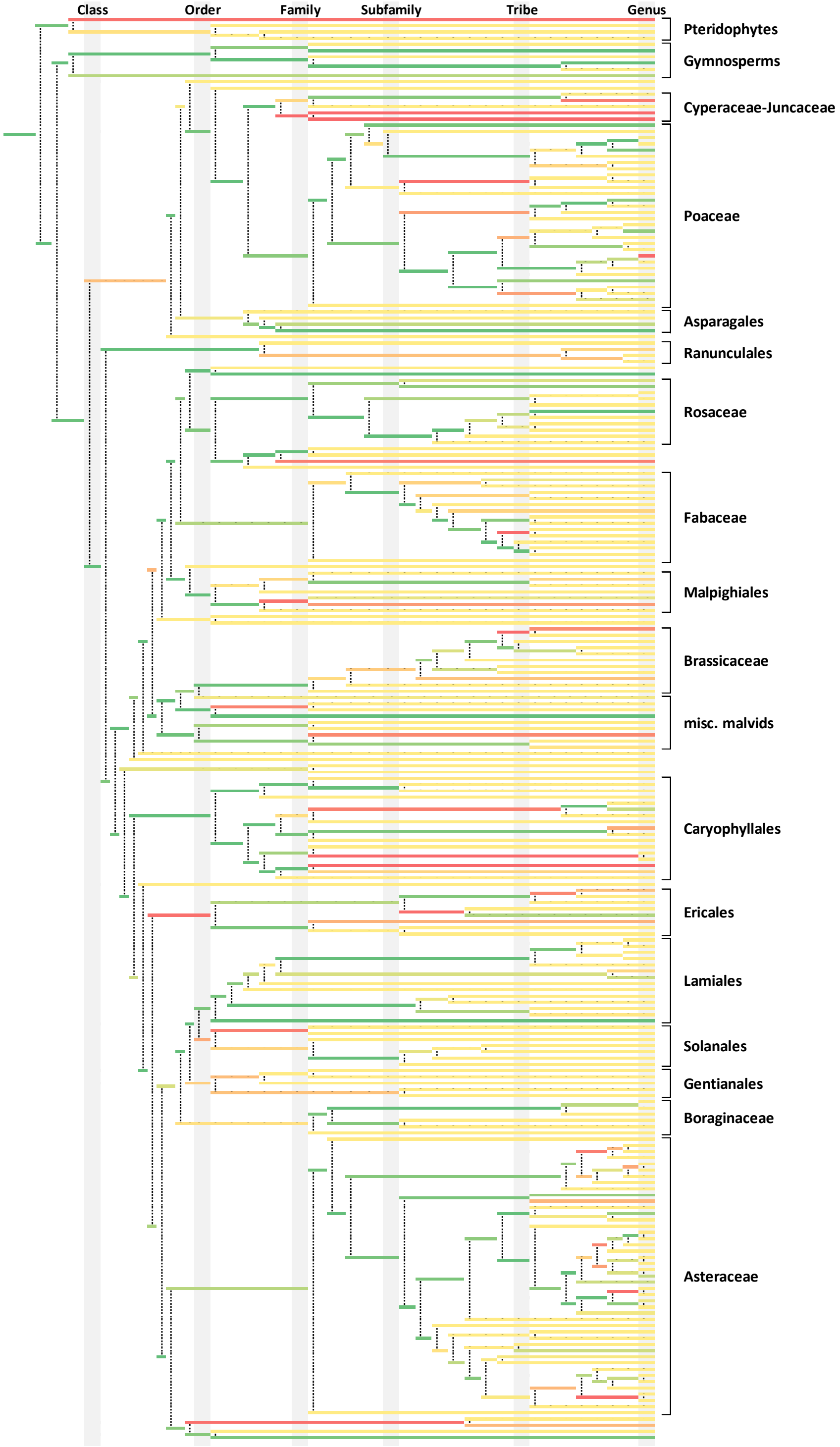

Figure 3.3. Results of **beta niche** overlap tests based on **presence/absence**, mapped onto a genus-level phylogeny of vascular plants of Zion National Park. Sister groups are subtended by colored branches ranging from green (higher segregation than expected) through red (higher aggregation than expected). Terminal branches are null (yellow) if they contain only one species, otherwise they are averages for congeneric species pairs (Appendix 3.2). See also Appendix 3.3.

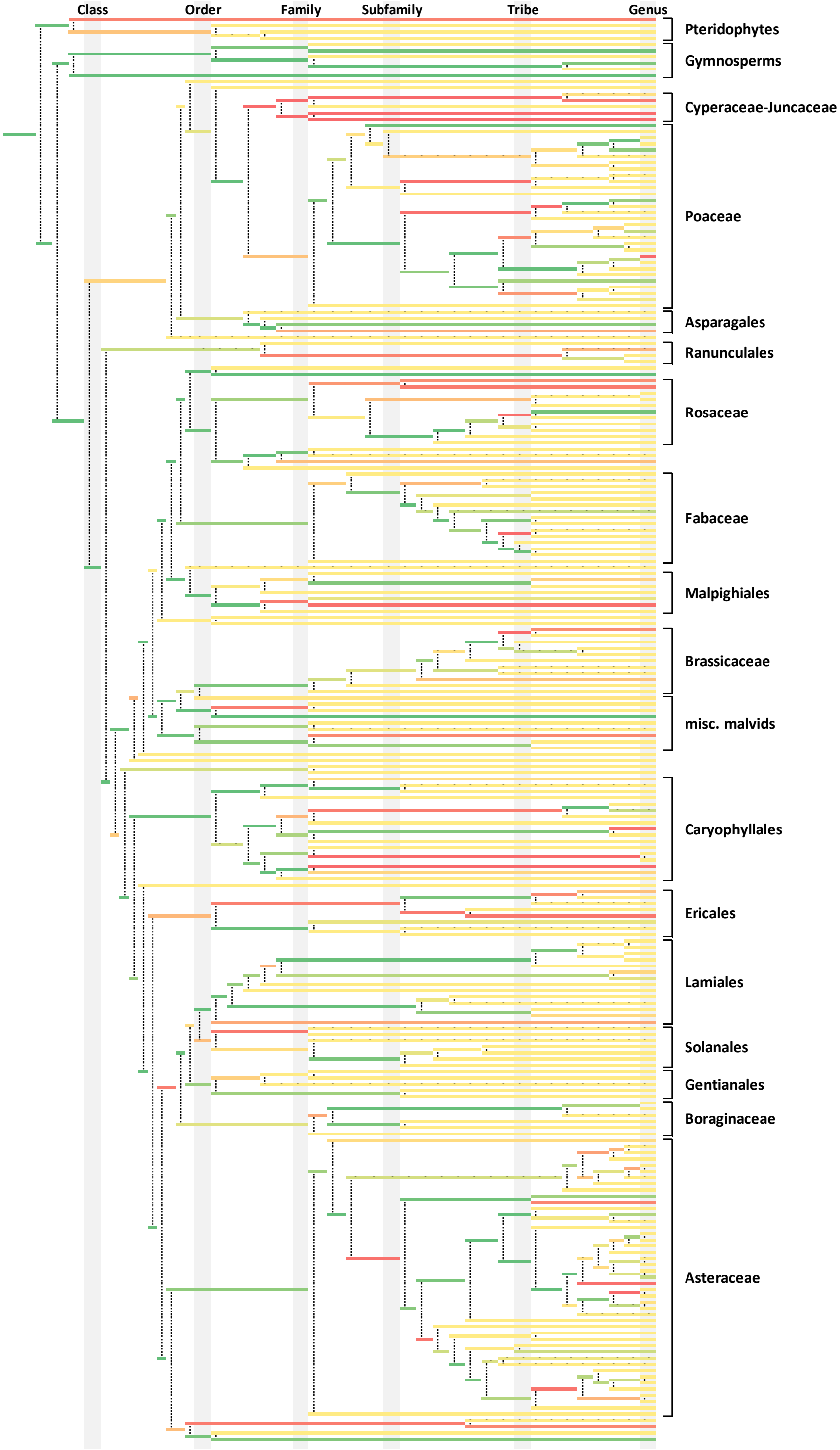

Figure 3.4. Results of **beta niche** overlap tests based on **cover**, mapped onto a genus-level phylogeny of vascular plants of Zion National Park. Sister groups are subtended by colored branches ranging from green (higher segregation than expected) through red (higher aggregation than expected). Terminal branches are null (yellow) if they contain only one species, otherwise they are averages for congeneric species pairs (Appendix 3.2). See also Appendix 3.3.

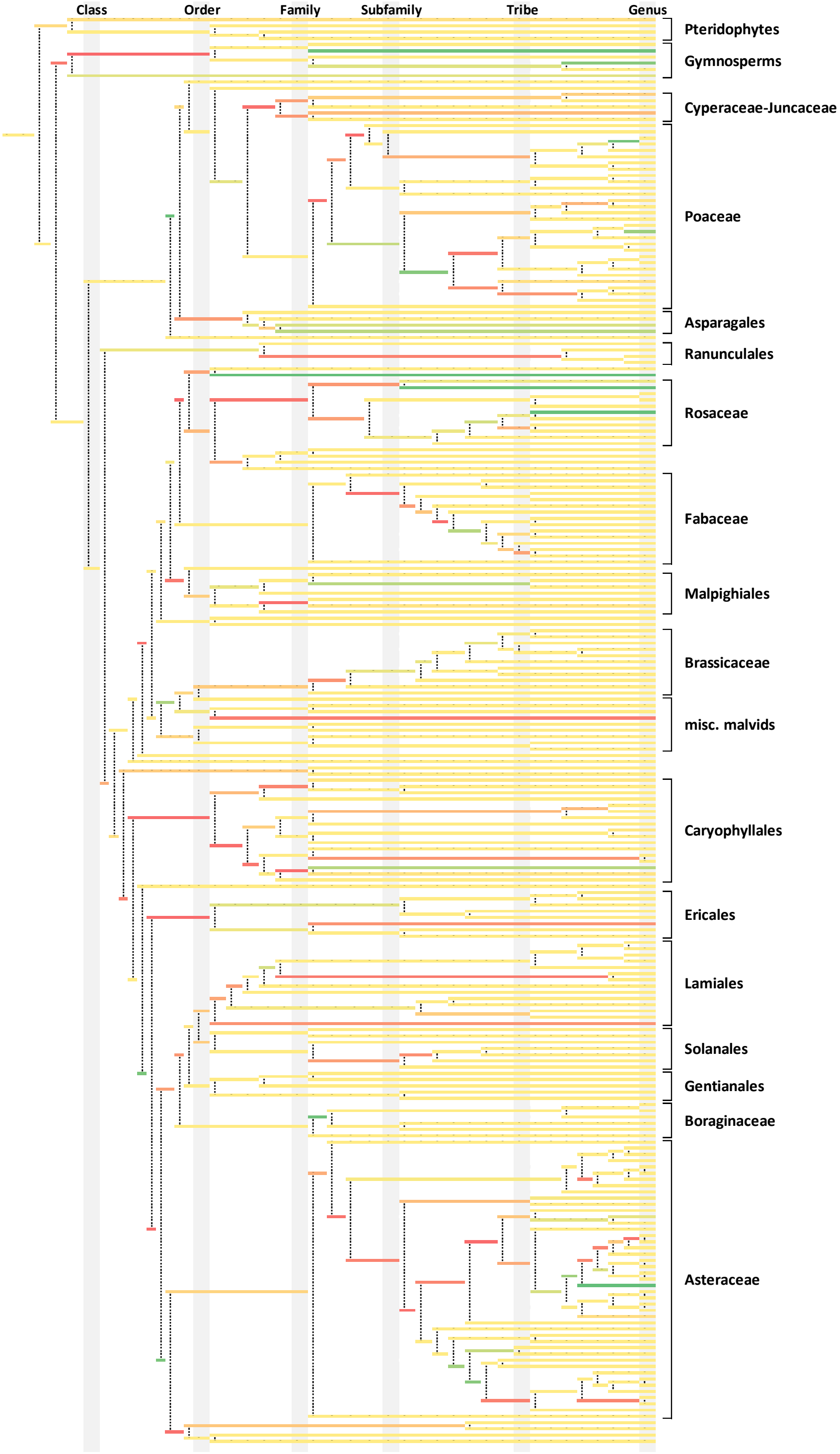

Figure 3.5. Results of **alpha niche** overlap tests based on **presence/absence**, mapped onto a genus-level phylogeny of vascular plants of Zion National Park. Sister groups are subtended by colored branches ranging from green (higher segregation than expected) through red (higher aggregation than expected). Terminal branches are null (yellow) if they contain only one species, otherwise they are averages for congeneric species pairs (Appendix 3.2). See also Appendix 3.3.

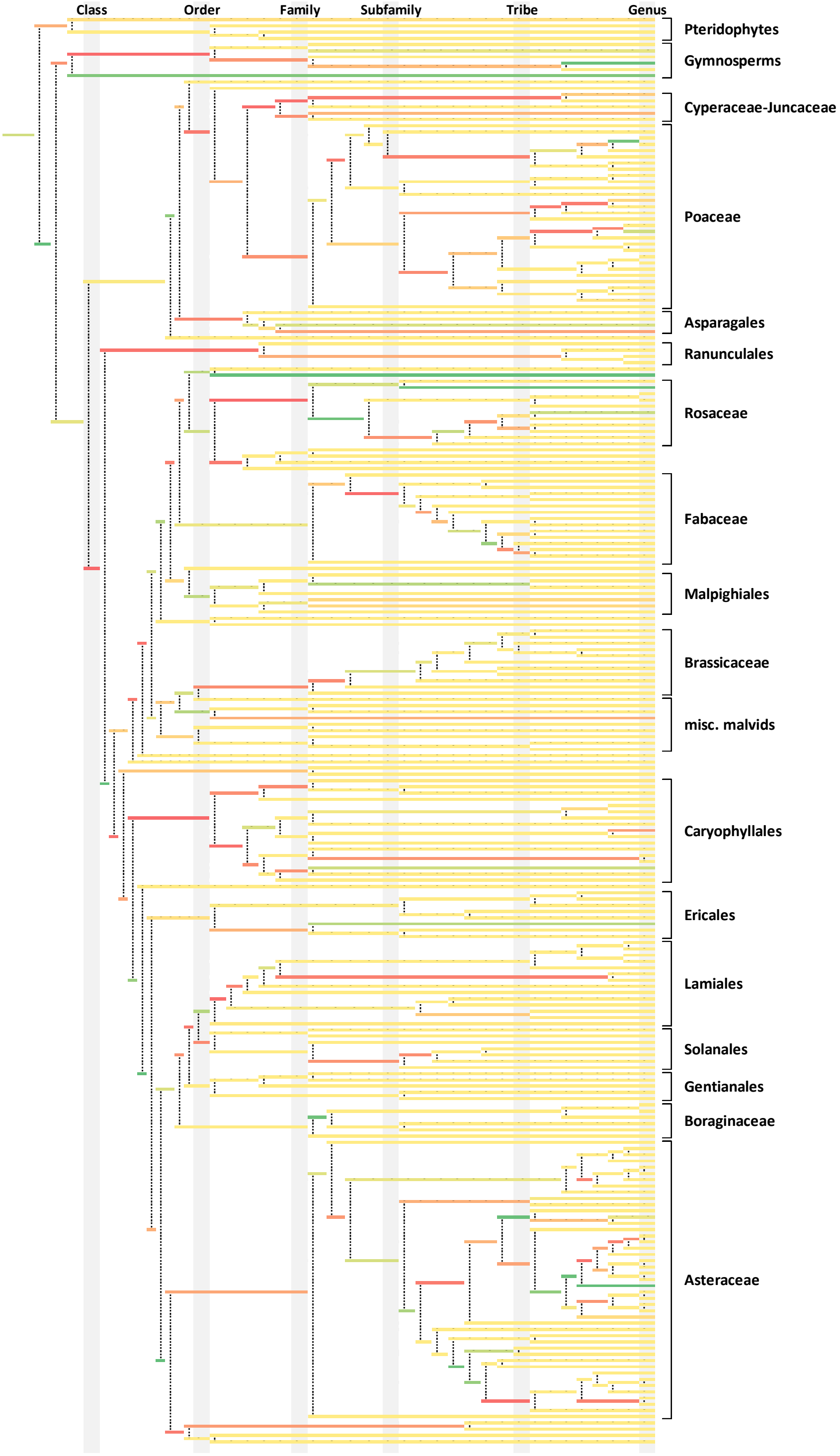

Figure 3.6. Results of **alpha niche** overlap tests based on **cover**, mapped onto a genus-level phylogeny of vascular plants of Zion National Park. Sister groups are subtended by colored branches ranging from green (higher segregation than expected) through red (higher aggregation than expected). Terminal branches are null (yellow) if they contain only one species, otherwise they are averages for congeneric species pairs (Appendix 3.2). See also Appendix 3.3.

Table 3.1. Ecological divisions used to group alliances of the U.S. National Vegetation Classification at Zion National Park.

Ecological Division	Alliances
Coniferous Forests	Douglas-fir Forest, White Fir Forest
Desert Shrublands	Blackbrush Shrubland, Fourwing Saltbush Shrubland, Nevada Joint-fir Shrubland, Painted Desert Sparsely Vegetated, Snakeweed Dwarf-shrubland
High Elevation Deciduous Forests	Bigtooth Maple Montane Forest, Quaking Aspen Forest, Quaking Aspen Temporarily Flooded Forest, White Fir - Quaking Aspen Forest
Higher Elevation Shrublands	(Stansbury Cliff-rose, Mexican Cliff-rose) Shrubland, Black Sagebrush Dwarf-shrubland, Gambel Oak Shrubland, Greenleaf Manzanita Shrubland, Mexican Manzanita Shrubland, Mountain-mahogany Sparsely Vegetated, Utah Serviceberry Shrubland
Lower Elevation Shrublands	Basin Big Sagebrush Shrubland, Big Sagebrush Shrubland, Rubber Rabbitbrush Sand Deposit Sparse Vegetation [provisional], Green Rabbitbrush Shrub Herbaceous, Mormon-tea Shrubland, Mountain Big Sagebrush Shrubland, Rubber Rabbitbrush Shrubland, Sand Sagebrush Shrubland, Turbinella Live Oak Shrubland
Pinyon/Juniper Woodlands	Rocky Mountain Juniper Woodland, Singleleaf Pinyon - (Utah Juniper) Woodland, Two-needle Pinyon - (Juniper species) Woodland, Utah Juniper Woodland
Ponderosa Pine Woodlands	Ponderosa Pine Woodland
Riparian/Wetland Vegetation	(Coyote Willow, Sandbar Willow) Temporarily Flooded Shrubland, (Field Horsetail, Variegated Scouringrush) Semipermanently Flooded Herbaceous, (Swollen-beak Sedge, Beaked Sedge) Seasonally Flooded Herbaceous, Arrow-weed Seasonally Flooded Shrubland, Emory Seepwillow Shrubland [provisional], Baltic Rush Seasonally Flooded Herbaceous, Box-elder Temporarily Flooded Woodland, Fremont Cottonwood Temporarily Flooded Forest, Fremont Cottonwood Temporarily Flooded Woodland, Nebraska Sedge Seasonally Flooded Herbaceous, Single-leaf Ash Temporarily Flooded Woodland, Strapleaf Willow Temporarily Flooded Shrubland, Water Birch Temporarily Flooded Shrubland
Slickrock Sparse Vegetation	Littleleaf Mountain-mahogany Sparsely Vegetated, Wooded Bedrock Sparsely Vegetated
Upland Grasslands	Blue Grama Herbaceous, Intermediate Wheatgrass Semi-natural Herbaceous, James' Galleta Herbaceous, Kentucky Bluegrass Semi-natural Seasonally Flooded Herbaceous, Mountain Muhly Herbaceous, Mountain Snowberry Shrubland, Needle-and-Thread Bunch Herbaceous, Sand Dropseed Herbaceous, Smooth Brome Semi-natural Herbaceous

Table 3.2. References used to resolve phylogenetic relationships within families for the genus-level vascular plant supertree used in the current study.

Family	References
Amaranthaceae	Flores and Davis 2001
Asteraceae	Miao et al. 1995, Noyes and Rieseberg 1999, Urbatsch et al. 2000, Baldwin et al. 2002, Panero and Funk 2002, Schilling and Panero 2002, Lee et al. 2003, Roberts and Urbatsch 2003, Urbatsch et al 2003, Valles et al. 2003, Beck et al. 2004, Roberts and Urbatsch 2004, Funk et al. 2005, Moore and Bohs 2007, Selliah and Brouillet 2008, Morgan et al. 2009, Panero and Funk 2008, Kilian et al. 2009
Boraginaceae	Langstrom and Chase 2002, Stevens 2008
Brassicaceae	Hauser and Crovello 1982, Beilstein et al. 2008, German et al. 2009
Cyperaceae	Muasya et al. 2009
Ericaceae	Stevens 2008
Fabaceae	Wojciechowski et al. 2004
Lamiaceae	Walker and Sytsma 2007, Moon et al. 2009
Nyctaginaceae	Douglas and Manos 2007
Pinaceae	Wang et al. 2000
Plantaginaceae	Albach et al. 2005
Poaceae	Duvall et al. 1994, Spangler et al. 1999, GPWG 2001, Duvall et al. 2001, Hilu and Alice 2001, Mason-Gamer 2005, Quintanar et al. 2007, Barkworth et al. 2008, Gillespie et al. 2008, Schneider et al. 2009
Polemoniaceae	Johnson et al. 2008
Polygonaceae	Sanchez et al. 2009
Ranunculaceae	Ro et al. 1997, Cai et al. 2009, Wang et al. 2009
Rosaceae	Potter et al. 2007
Solanaceae	Martins and Barkman 2005

Table 3.3. Summary of niche overlap tests for congeneric pairs and phylogenetic sister groups (genus and above) of vascular plant species at Zion National Park. Numbers of cases of aggregation (higher overlap than expected), segregation (lower overlap than expected) and null (neither higher nor lower overlap than null models) are shown, along with numbers of significant cases (p<0.05 for two-tailed test) in parentheses. See Appendices 3.2-3.3 for full detail.

A. Congeneric Pairs		**Aggregation**	**Segregation**	**Null**
Beta Niche Overlap	Presence	123 (42)	151 (30)	67
	Cover	141 (34)	129 (24)	71
Alpha Niche Overlap	Presence	44 (7)	41 (8)	256
	Cover	45 (9)	38 (7)	258

B. Sister Groups		**Aggregation**	**Segregation**	**Null**
Beta Niche Overlap	Presence	52 (7)	164 (67)	15
	Cover	64 (10)	152 (62)	15
Alpha Niche Overlap	Presence	94 (14)	42 (1)	96
	Cover	96 (9)	56 (6)	79

CHAPTER 4

SHARPENING THE FOCUS OF COMMUNITY PATTERNS BY ADJUSTING PHYLOGENETIC SCALE

ABSTRACT

Scale is an important issue in community ecology because community patterns differ according to the scale of observation. Spatial scale determines which taxa are captured and which spatial phenomenon are highlighted in community analysis. If community-environment relationships are the phenomenon of interest, the influence of ecological interactions at a small spatial grain (i.e., small sample unit size) or species dispersal limitation at a large spatial extent (i.e., large sampled area size) could be considered noise. Here I consider the possibility that these types of noise can be reduced by adjusting the phylogenetic scale of analysis. Phylogenetic scale can be defined in a manner similar to spatial scale, defining extent as the phylogenetic scope of a community study (e.g. vascular plants) and grain as the phylogenetic resolution of community units (e.g. species). Focus, another spatial scale concept referring to sample unit averaging, can also be applied to taxa in the form of phylogenetic lumping. Lumping of phylogenetically-related taxa may be appropriate if the taxa exhibit phylogenetic niche conservatism and thus respond to environmental gradients in similar ways, even though they may be spatially segregated due to ecological interactions or historical factors. Under these conditions the effectively coarser phylogenetic grain of lumped taxa could

sharpen community-environment patterns under the constraints of a given spatial grain and extent. This raises the question of how to identify such an “optimal” phylogenetic grain, given that patterns of niche conservatism may differ in different lineages and on different environmental gradients. I suggest a solution that entails exploratory analysis of association patterns among taxa at multiple levels of a phylogenetic hierarchy, leading to identification of clusters of strongly-associated taxa of potentially variable phylogenetic resolution. This approach follows the logic of indirect gradient analysis by using community patterns to infer environmental influences while also reducing potential noise arising from the use of a fixed community taxonomic level. I present an application of this approach using data from the Carolina Vegetation Survey.

INTRODUCTION

For many years, community ecologists have sought to characterize communities based on patterns of selected taxa within defined study areas. Taxonomically-based, spatially-defined community characterization is exemplified by studies employing classification or ordination techniques (McCune and Grace 2002) to elucidate patterns of spatial variation in species composition of a targeted taxonomic group in a study area of interest. For example, vascular plants have been a commonly-targeted taxonomic group for studies in which the presence or abundance of species in sample plots has been used to classify or ordinate plant communities of local to regional study areas (Mueller-Dombois and Ellenberg 1974, Kent and Coker 1992, Jennings et al. 2009).

An implicit assumption of such studies is that spatial variation in species composition (presence and/or abundance) is due, at least in part, to environmental factors that also vary spatially within the study area. Identifying the environmental factors responsible for community patterns is a common objective that is frequently pursued using correlative approaches. Correlative relationships between community patterns and environmental variables may be difficult to detect because the relevant environmental factors are difficult to measure, or because chance events contribute to noisy patterns (McCune and Grace 2002). Another possible reason for weak community-environment relationships, which forms the topic of this paper, is that community patterns are often described from an inappropriate scale. In particular, I consider the often overlooked issue of phylogenetic scale.

As used here, the term phylogenetic scale refers to the manner in which a set of taxa are indexed relative to an evolutionary hierarchy. The hierarchy could be based on a taxonomic classification system, in which case the term taxonomic scale would also apply, or the more explicit hierarchy of a phylogenetic tree model. Although similar concepts have been discussed under other names for many years, references to phylogenetic or taxonomic scale have appeared relatively recently in the community ecology literature (e.g. Williams et al. 1994, Roberts and Cohan 1995, Saiz-Salinas and Gonzalez-Oreja 1999, Pandolfi 2001, McGill et al. 2005, Oline 2006, Slingsby and Verboom 2006). Different authors have used these terms in different ways, suggesting a need for standardized usage and more specific terminology. A similar problem of ambiguous usage led the more widely-discussed spatial scale concept to be defined more explicitly in terms such as extent, grain and focus (Wiens 1989, Scheiner et al. 2000). One of the objectives of this paper is to clarify the meaning of phylogenetic scale by drawing parallels with these spatial scale concepts.

Both spatial scale and phylogenetic scale are important in community-environment studies because they jointly determine which evolutionary and ecological processes are highlighted by community patterns. If the highlighted processes are not relevant to the environmental variables of interest, they contribute to noise that dilutes the strength of correlative relationships. This paper uses conceptual models to illustrate the effects of interacting ecological and evolutionary processes on community patterns, including processes that may contribute to noise when community-environment relationships are the pattern of interest. I then consider the implications of adjusting an easily-manipulated component of phylogenetic scale—the phylogenetic grain, or resolution—for bringing community-environment relationships into sharper focus.

The idea that community patterns may be in sharper focus at some phylogenetic scales than others led to the development of an exploratory analysis technique capable of examining community patterns at multiple levels of a phylogenetic or taxonomic hierarchy. This technique, as introduced and applied in this paper, is a modification of species clustering expanded to allow taxa (or clades) above the species level to be included in clusters. Although environmental variables are not used directly in the clustering process, the clusters identified through this technique represent taxa with similar distributions that are likely to be correlated with one or more environmental variables at the spatial scale defined for the analysis. This technique is demonstrated here for a set of plant communities of the Southern Appalachian Mountains, U.S.A. using data from the Carolina Vegetation Survey (Peet et al. 1993).

Each section of this paper covers one of the stated objectives, namely to (1) clarify the meaning of phylogenetic scale by drawing parallels with spatial scale concepts of extent, grain and focus; (2) elucidate ecological and evolutionary processes that can be inferred at various spatial and phylogenetic scales; (3) explain how noise in community-environment relationships can potentially be reduced by refocusing the phylogenetic grain; (4) introduce an exploratory analysis approach for phylogenetic refocusing of community patterns; and (5) demonstrate an application of phylogenetic refocusing using plant community data from the Carolina Vegetation Survey.

1. SCALE CONCEPTS: EXTENT, GRAIN AND FOCUS

Taxa in a community sample can be arranged in a nested hierarchy of evolutionary ancestry just as community sample units can be arranged in a hierarchy of spatial proximity. The similar hierarchical structure allows spatial scale concepts of extent, grain and focus to be logically translated into phylogenetic scale concepts (Fig. 4.1-4.2).

Spatial extent refers to the sampled spatial universe, e.g. the area covered by a set of plots (Fig. 4.1a) (Wiens 1989, Palmer and White 1994). By analogy, phylogenetic extent is that portion of the evolutionary universe covered by a community study (Fig. 4.1b). Major taxonomic groups traditionally used to define communities (vascular plants, mammals, arthropods, etc.) exemplify this concept[2]. By this general definition phylogenetic extent would include all members of a specified group sharing a common ancestor, but in reality only a subset of the group will be represented: extant taxa residing within the spatial extent that are captured by sampling (Ackerly 2000, Webb et al. 2002). This definition of phylogenetic extent corresponds with recent usage of the terms

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[2] Communities can also be defined without reference to phylogeny, e.g. in food web studies. Here I follow the tradition of taxonomically/trophically defined communities.

“phylogenetic scale” and “taxonomic scale” in studies of community phylogenetic structure (Cavender-Bares et al. 2006, Slingsby and Verboom 2006, Swenson et al. 2006).

Phylogenetic grain likewise draws its meaning through analogy with its spatial counterpart. Spatial grain refers to the size of sample units, such as the two-dimensional area of plant community plots (Fig. 4.1a) (Wiens 1989, Palmer and White 1994). The equivalent “sample units” of the evolutionary hierarchy are operational taxonomic units (OTUs) that serve as the currency of biodiversity in community studies (Kelt and Brown 2000, Schloss and Handelsman 2006), and the “size” of the OTUs is related to their position in the hierarchy. Phylogenetic grain can be defined as the level of phylogenetic resolution of OTUs, commonly expressed as a taxonomic rank (Fig. 4.1b). Community ecologists have traditionally used species as the taxonomic rank of choice, reflecting the importance placed on species in taxonomy, natural history and evolutionary biology (Kelt and Brown 2000, Rieseberg and Burke 2001, Sites and Marshall 2003). However, OTUs at levels of phylogenetic resolution above species (genera, families, phyla, etc.) or below (subspecies, varieties, ecotypes, etc.) have also found their place in community studies (e.g. Moral and Denton 1977, Deil 1989, Deil 1994, Kuerschner and Parolly 1999).

In principle, members of any taxonomic rank could be used for community OTUs provided they correspond to ecologically-meaningful units. Furthermore, the OTUs need not all reside at the same taxonomic rank, given that ranks do not necessarily convey a consistent ecological meaning for different groups classified by different taxonomists (Bachmann 1998). In practice, the taxonomic rank or level of phylogenetic resolution may differ among different groups within a community study according to the ease with which taxonomic identities can be specified. The commonly-discussed tradeoff between taxonomic specificity and time investment in community studies (Beattie and Oliver 1994, Williams and Gaston 1994, Pik et al. 1999, Saiz-Salinas and Gonzalez-Oreja 1999) can be framed as an issue of phylogenetic grain.

Focus is another spatial scale concept referring to a level of sample unit aggregation (Scheiner et al. 2000). Sample units within some level of spatial proximity can be aggregated and averaged, effectively increasing the spatial grain size. When applied to phylogenetic scale, this translates into lumping of taxa; phylogenetic focus is the level at which taxa are lumped. Many studies have applied the phylogentic focus concept by analyzing communities at taxonomic ranks higher than the level of recorded OTUs (Dale and Clifford 1976, Dale et al. 1989, Ferraro and Cole 1992, Somerfield and Clarke 1995, Bowman and Bailey 1997, Chapman 1998, Olsgard et al. 1998, Doledec et al. 2000, Mistri and Rossi 2000, Metzeling et al. 2002, Narayanaswamy et al. 2003, Anderson et al. 2005a, Anderson et al. 2005b). Phylogenetic focus could also conceivably involve aggregation to a level defined by branch length distance on a phylogenetic tree. Phylogenetic aggregation to either a uniform taxonomic rank or a consistent branch length distance are both examples of what I define as rigid phylogenetic focus, analogous to rigid spatial focus where sample units are aggregated within a specific spatial distance (Fig. 4.2a-b). Alternatively flexible focus, whether spatial or phylogenetic, is not based on external distance constraints but allows other criteria to guide the aggregation process, possibly resulting in units aggregated to different distances in different spatial or phylogenetic zones (Fig. 4.2c-d). The flexible focus concept is central to the analysis approach presented below (Sections 3-5).

2. PROCESSES LINKED TO SPATIAL AND PHYLOGENETIC SCALE

Community patterns at various spatial and phylogenetic scales can be linked to ecological and evolutionary processes operating at various temporal scales. For conventional communities composed of species (as the phylogenetic grain) within a taxonomic group (the phylogenetic extent), ecological processes of interest include species interactions and environmental filtering, which operate on shorter temporal scales than species-level evolutionary processes such as speciation and niche divergence.

At small spatial scales, one would expect to see the imprint of recent ecological processes resulting in combinations of species that are adapted to local environmental conditions and compatible with one another. Species with similar alpha-niches (similar interactive effects in a local community) would be expected to have limited compatibility, and thus rarely co-occur, while species with similar beta-niches (similar environmental tolerances and affinities) would be expected to be found together (Silvertown et al. 2001, Webb et al. 2002, Silvertown 2004, Silvertown et al. 2006).

Niche attributes of species are ultimately the result of evolutionary niche divergence over longer time scales. Within an evolving lineage, divergent niches may arise among related species as they diverge genetically, although ancestral niches might alternatively be retained through niche conservatism (Harvey and Pagel 1991, Webb et al. 2002). Niche conservatism leads to a correspondence between phylogenetic relatedness and niche attributes that should lead to patterns of local aggregation or segregation of related species, depending on whether the alpha or beta niche (or both) is conserved (Webb et al. 2002, Cavender-Bares et al. 2004, Cavender-Bares et al. 2006). More precisely, related species with conserved beta niches are likely to be segregated at small-grain spatial scales if their alpha niches are conserved, but may be aggregated if their alpha niches are divergent (Fig. 4.3a, left column). If beta niches are not conserved, the alpha niche becomes irrelevant for small-grain patterns because the species are segregated into different environments where they do not interact (Fig. 4.3a, right column). Likewise, if species are not sympatric at the broader scale of their geographic ranges, small-grain aggregation will not be observed (Fig. 4.3b). However, allopatric species with conserved beta niches will likely occupy similar environments in their respective ranges (Fig. 4.3b, left column). Conserved beta niches can thus be said to result in aggregation by habitat, regardless of segregation patterns at small grain sizes or large spatial extents (Fig. 4.3).

The terms allopatric and sympatric are commonly associated with species-level genetic divergence processes (speciation), but are also more broadly applicable to divergence at any phylogenetic level. Allopatric divergence may be evident in spatially-segregated populations both prior to and following speciation, although the pattern may eventually be obscured by range shifts resulting in secondary contact of the divergent species (Barraclough and Vogler 2000, Barraclough and Nee 2001, Losos and Glor 2003). For the purposes of the model presented here, the terms allopatric and sympatric are defined empirically based on current distributions regardless of historical origins. As such, portions of a taxon's range may be sympatric and other portions allopatric with regard to a related taxon. The relevant point is that allopatric ranges may sometimes segregate related taxa that are, because of phylogenetic niche conservatism, ecologically similar. This becomes an issue when the spatial extent of a community study spans the ranges of such taxa.

Phylogenetic niche conservatism can likewise be defined empirically based on contemporary niche similarity of related taxa (cf. Webb et al. 2002), bypassing the species-level historical meaning sometimes associated with the term (Harvey and Pagel 1991). By expanding the niche conservatism concept beyond the species level, patterns of phylogenetic niche similarity can be considered for any set of related taxa or clades, i.e. at alternative phylogenetic grain sizes. Implications of alternative phylogenetic grain sizes on community pattern and process detection are considered further in the following section.

3. REFOCUSING THE PHYLOGENETIC SCALE OF COMMUNITY PATTERNS

As described in the previous section, spatial segregation of related taxa may occur at a small spatial grain because of alpha-niche similarities, or at a large spatial extent because of allopatric divergence. In addition, patterns of taxa in community samples can be attributed to an element of chance in which species end up at which sites (Gilbert and Lechowicz 2004, Bell 2005, Karst et al. 2005) and which sites end up being sampled. While these patterns and processes are of interest for their own sake, they constitute noise when the objective is to discover community patterns related specifically to the process of environmental filtering. Community classification studies, for example, commonly aim to define communities based on sets of species that jointly occupy similar habitats. If certain species are incompatible at the spatial grain of sampling, if certain species are missing from portions of the spatial extent, or if certain species are erratic in their distribution, the consistency of species occupying the habitat(s) of interest will be compromised.

Figure 4.4 illustrates this point through a hypothetical scenario in which community composition has been sampled at multiple locations spanning a large spatial extent. Each sample plot in Figure 4.4 captures the environmental conditions of a specific habitat that is scattered throughout the extent of the study area. However, the species composition of these plots, as illustrated by letters in Figure 4.4a, is not consistent across the area. Species A represents a widespread, frequently-encountered species, the only species present in all plots. Species B-F are geographically-restricted congeners whose ranges do not overlap because of recent allopatric speciation events. Species G-H are sympatric and widespread but are not found in close proximity because of alpha-niche conservatism resulting in resource competition. Lastly, species J-M have partially-overlapping ranges and seemingly random plot occupancy and abundance, suggesting neutral community assembly processes (Bell 2005).

If the phylogenetic grain is refocused, as illustrated in Fig. 4.4b, each of these clades (A, B-F, G-H, and J-M) is found to be present, in roughly equal proportions, in each of the plots. The conclusion to be drawn is that species within each clade have conserved beta-niches (relative to the habitat under study) and are thus suitable units for characterizing the community at the given spatial grain and extent. Noise is eliminated in this scenario as the phylogenetic grain of analysis is refocused from the species level to higher phylogenetic levels (with the exception of species A, which did not require refocusing to reach maximum consistency). Because the refocused levels are not constrained to a single taxonomic rank or uniform branch length distance across all lineages, this is an example of flexible phylogenetic refocusing (Section 1).

4. AN EXPLORATORY APPROACH FOR PHYLOGENETIC REFOCUSING

For real datasets, refocusing phylogenetic grain size by lumping species to an optimal, lineage-specific level may not be as simple as the hypothetical scenario shown in Figure 4.4. The hypothetical scenario considered only a single habitat instead of the multiple habitats likely to be included in a typical community classification study. Furthermore, discrete habitats may not easily be defined, especially if environmental variables are difficult to measure and/or occur as continuous gradients across the landscape. Patterns of beta-niche conservatism inferred from habitat occupancy will obviously depend on how the habitat is defined; different patterns of niche conservatism could conceivably be seen along different environmental gradients. Also, the empirical limits of niche conservatism (as drawn by the refocus line in Fig. 4.4b) may not be clearly marked in a phylogenetic hierarchy, especially in lineages where ecological traits have evolved gradually. There may not be a single ‘optimal’ phylogenetic focus where noise is reduced to the degree illustrated in Fig. 4.4b because of random or individualistic patterns of some taxa in relation to environmental gradients. All these complicating issues need to be taken into account when attempting to apply phylogenetic refocusing to real-world community analysis.

The community analysis technique introduced here addresses these issues by taking an exploratory approach for identifying community patterns at multiple levels of a phylogenetic hierarchy. The need for *a priori* habitat characterization is circumvented by using community patterns themselves to define classes or axes of environmental variation, a principle that has been routinely followed in community clustering and indirect gradient analysis (Kent and Coker 1992, Jongman et al. 1995, McCune and

Grace 2002). By analyzing a species/sample unit matrix on its own, then relating it to environmental variables secondarily, the species ‘inform’ the analyst about the environment as ‘seen’ from their own perspective. In the technique presented here, this type of analysis is expanded so that, in addition to species, other phylogenetic units (higher taxa or clades) can contribute to community patterns. The technique identifies combinations of phylogenetic units yielding the strongest community patterns given the data and the criteria supplied by the analyst (see below). By quantifying the strength of the pattern and rejecting weak patterns as noise, this technique accommodates the reality that not all lineages are likely to exhibit phylogenetic niche conservatism nor are all taxa likely to offer informative information about community-environment relationships.

The new analysis technique is a modified version of Coalition Clustering, a non-hierarchical agglomerative clustering algorithm that was designed to identify clusters of positively-associated species in community datasets (Sanderson et al. 2006). The Coalition Clustering algorithm iteratively joins species meeting a user-specified significance criterion into clusters. The significance criterion is a threshold level of mean pairwise association[3]. Clusters are built as species in the dataset are drawn in random order, the first species initiating the first cluster and subsequent species either being added to existing clusters or initiating new clusters. Species can be added to multiple existing clusters but cannot initiate new clusters if they can be added elsewhere. The clusters are progressively refined by combining similar clusters, adjusting their

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[3] Pairwise association is based on a two-by-two contingency table of presence/absence. Asociation coefficients such chi-square and phi utilize information from all four cells of the table including joint absences. Although described here in terms of association, Coalition Clustering can also be carried out using co-occurrence indices that omit joint absences (e.g. Jaccard Index, Sorensen Index) or correlation coefficients that allow the use of abundance information (e.g. Pearson’s R) (Ludwig and Reynolds 1988).

composition and weeding out single-species clusters until a stable set of clusters is obtained. Changing the significance criterion affects the size and number of clusters; a stringent criterion tends to produce many clusters containing few species, while a relaxed criterion tends to produce few clusters containing many species (Sanderson et al. 2006). Species belonging to clusters can be viewed as characteristic species of abstract (compositionally-defined) community types, which can then be used to characterize concrete (spatially-defined, albeit not necessarily discrete) communities based on the degree to which site species composition resembles cluster composition. Concrete community characterization opens the door for correlative analysis between coalition clusters and environmental variables (Sanderson et al. 2006).

The modified version of Coalition Clustering, referred to as Multilevel Ordered Coalition Clustering (MOCC) differs from the original algorithm described by Sanderson et al. (2006) in two principal ways. First, it incorporates an ordered clustering strategy that builds a cluster for each species in the dataset, using each species to initiate a cluster and then adding other species one at a time in descending order of association strength (S.C. Sanderson, pers. comm.). New species are added to each cluster, or removed as needed, until no more species meet the significance criterion. Some species may fail to accrete clusters and such species are removed. Once a cluster has been built for each eligible species, the set of unique clusters can be examined and, if desired, similar clusters can be merged. This procedure has the advantage of providing a unique clustering solution, in contrast to the random accretion procedure of the original Coalition Clustering algorithm for which the solution can vary under identical settings.

The second way in which MOCC differs from the original Coalition Clustering algorithm is by allowing higher taxa or clades to enter into clusters alongside species (hence the prefix ‘multilevel’). This is not a trivial addition to the algorithm, despite the fact that species occurrences can be easily converted to higher taxon/clade occurrences if an appropriate phylogeny or classification hierarchy is available. The challenge arises in building clusters that do not contain phylogenetically-redundant information, as would be the case if a species, plus the genus, family, etc. to which it belongs, were included in the same cluster. Avoiding this situation requires specifying which taxa/clades (hereafter ‘units’) are phylogenetically independent, i.e. not overlapping members of the same lineage. Figure 4.5 illustrates how a pairwise species association matrix can be expanded to a multilevel matrix with non-independent pairwise association values removed. Such a matrix is suitable for selecting the first pair of units in a cluster, but before subsequent units can be added the matrix must be re-filtered to exclude all units that are not independent from either unit of the intitial cluster pair. Each addition or subtraction of a unit from each cluster requires a re-assessment of which pairwise association values are phylogenetically independent. The order in which units are accreted to a cluster has a cascading effect on the accretion eligibility of the remaining units. In consequence of these features of the multilevel algorithm, many different combinations of units are possible for clusters that are actually compositionally similar under the surface. There is no easy way to merge compositionally-similar multilevel clusters if they contain phylogenetically non-independent variants of the same lineages; thus the multilevel algorithm (as currently configured) leaves clusters unmerged and allows the analyst to visually compare and screen them as needed.

5. APPLICATION OF PHYLOGENETIC SCALE REFOCUSING FOR SOUTHERN APPALACHIAN PLANT COMMUNITIES

As a simple demonstration of the phylogenetic refocusing analysis approach described above, I present an application of MOCC to a plant community dataset from the Carolina Vegetation Survey (Peet et al. 1993). A dataset of 219 vegetation survey plots was selected representing two habitats in the Southern Appalachian Mountains (USA): high elevation rock outcrops (Wiser et al. 1996) and mountain bogs (Wichmann 2009) (Figure 4.6). This dataset captures the contrasting habitats of the drier, exposed outcrops and the wetter, more sheltered bogs, which are known to harbor different plant communities. The Southern Appalachian Region is also known for having geographically-variable plant species composition that cannot easily be correlated with environmental variables at the regional extent scale (Newell et al. 1995, Nekola and White 1999). Species composition of outcrops and bogs would be expected to be particularly variable between different sites because of the insular, spatially restricted distribution of these habitats. Restricted geographical ranges, species incompatibilities and random community assembly could all contribute to within-habitat species compositional variation. By applying the phylogenetic refocusing approach to these communities, one can investigate whether such noisy variation within habitats can be offset by expanding the phylogenetic grain size beyond the species level.

The 623 OTUs represented by this dataset (primarily species, but also some higher taxa that were not identified to the species level) were placed in a taxonomic hierarchy based on the classification schemes of Weakley (2006) for the genus level and below, and NCBI (2008) above the genus level. Although not strictly phylogenetic, these classification schemes incorporate findings of recent phylogenetic systematic studies for large numbers of taxa, and hence are useful sources of evolutionary relationship information at a broad phylogenetic extent.

Pairwise association values for taxa at each level of the taxonomic hierarchy were calculated using the phi coefficient (Ludwig and Reynolds 1988). The pairwise association matrix was then fed into the MOCC algorithm, programmed using the R package for statistical computing (R Development Core Team 2008). A subset of clusters extracted at a significance level of phi=0.2 are shown in Table 4.1. The analysis revealed strong associations among groups at different phylogenetic levels as allowed under the flexible phylogenetic focus principle. Within single clusters were found multiple levels including orders, families, tribes, genera, subgenera, sections, species, and varieties. Clusters of taxa characteristic of rock outcrops were distinguishable from bog clusters based on *a priori* knowledge of bog and rock outcrop communities. In addition, some clusters appear to represent taxa common to both habitats (Table 4.1, General Bog + Rock Outcrop Cluster). The MOCC technique proved useful for highlighting community differences as well as commonalities, with flexible phylogenetic focusing revealing stronger patterns than would be captured in a strictly species-level analysis, given the spatial scale of the dataset.

CONCLUSION

Describing phylogenetic scale in terms of grain, extent and focus provides a useful conceptual framework for understanding issues related to taxonomic resolution in community studies. Community analysis using species or other fine-grained taxonomic units may introduce unnecessary noise that can be dampened by lumping taxa to a higher phylogenetic grain. This resembles the practice of grouping species into guilds, functional groups or trait-based groups (Wilson 1999, Duckworth et al. 2000, Pillar and Sosinski 2003), but does not require trait information beyond phylogenetic relationships. Trait-based groups may be more amenable to certain questions related to, for example, ecosystem attributes, or when comparing communities at intercontinental scales were niche conservatism is overshadowed by convergence of members of different lineages that have evolved similar adaptations to similar environments.

The flexible phylogenetic grain approach also offers advantages over current phylogenetic community analysis methods requiring branch length information and rigid phylogenetic grain (e.g. Webb et al. 2008). Reliable branch length information is often difficult to obtain for "supertrees" representing all members of a community at their highest phylogenetic resolution (Sanderson and Driskell 2003). In contrast, a supertree lacking branch length information is relatively easily to assemble, with taxonomic classification systems offering a default in the absence of more detailed data. Although the branch length difficulty is likely to diminish as phylogenetic systematics continues to progress, the value of branch length information in the ecological context remains an open question. The degree of ecological divergence is sometimes but not always correlated with the degree of genetic divergence between taxa (cf. Losos 2008). This perspective lends itself to the phylogenetic community analysis approach I have presented, which seeks to identify the position of ecological discontinuities in the phylogenetic hierarchy rather than examine the correlative relationship between phylogenetic distance and ecological variables.

Issues of spatial and phylogenetic scale are of particular importance as the scope of community studies expands to encompass larger areas and greater numbers of taxa. Databases of consolidated community samples drawn from multiple studies are increasingly available for analyses aimed at characterizing and understanding community variation (Mucina et al. 1993, Peet et al. 1993, Bruelheide and Chytry 2000). As the spatial extent of community analysis expands to encompass geographic turnover in species ranges, ecologists should consider whether the species level (or any other standard taxonomic rank) is the optimal phylogenetic grain for their analysis. Even in studies carried out at a more local scale, the implications of α-niche conservatism on segregation of closely-related species should be considered in the selection of spatial and phylogenetic grain. In some cases it may be feasible and appropriate to take the phylogenetic focus concept in the opposite direction, breaking OTUs into even finer units than have been presented here, such as haplotypes or genotypes.

The principles and techniques of phylogenetic grain adjustment presented here could also be extended to spatial grain adjustment, providing an alternative to autocorrelative approaches for analyzing spatial influences on sample units (Lichstein et al. 2002, Perry et al. 2002, Podani and Csontos 2006). Rigid phylogenetic re-focusing is conceptually analogous to merging sample units within a zone of spatial autocorrelation as identified through correlograms or semivariograms (Rossi et al. 1992, Wagner 2003). Flexible phylogenetic refocusing, by similar analogy, corresponds to spatial autocorrelation techniques that recognize non-stationarity, or differences in the strength of spatial autocorrelation that differ by location (Osborne et al. 2007). Identifying zones of “spatial community conservatism” due to high dispersal and low environmental variation, separated by zones of “spatial community divergence” due to opposing processes, is an avenue where parallels between spatial and phylogenetic scale could potentially complement one another.

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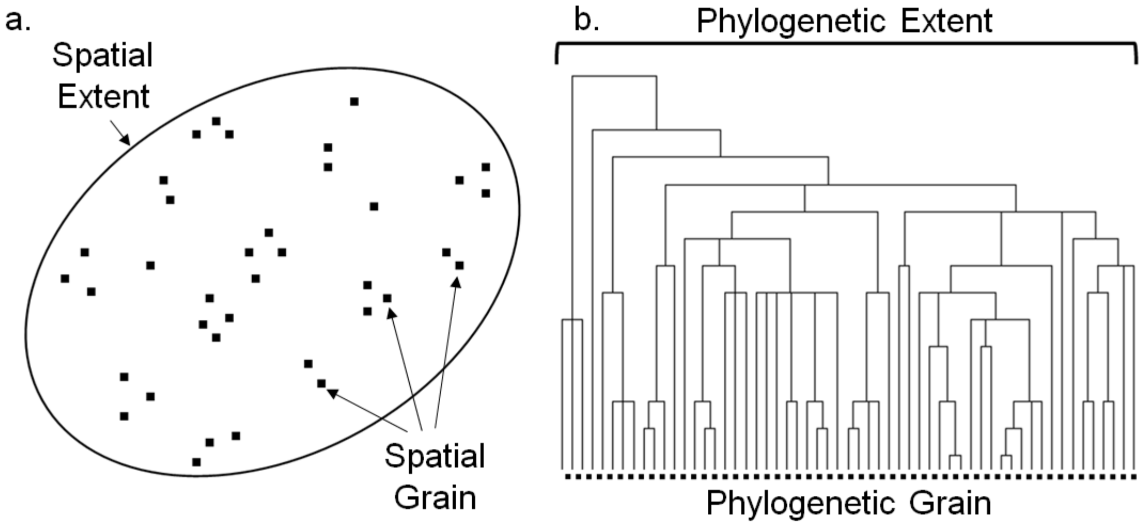


Figure 4.1. Conceptual parallels between spatial scale and phylogenetic scale of community studies: extent and grain. Spatial extent is the entire area covered by sampling; spatial grain the size of sample units (a). By analogy, phylogenetic extent is the entire lineage sampled; phylogenetic grain the resolution of operational taxonomic units (b).

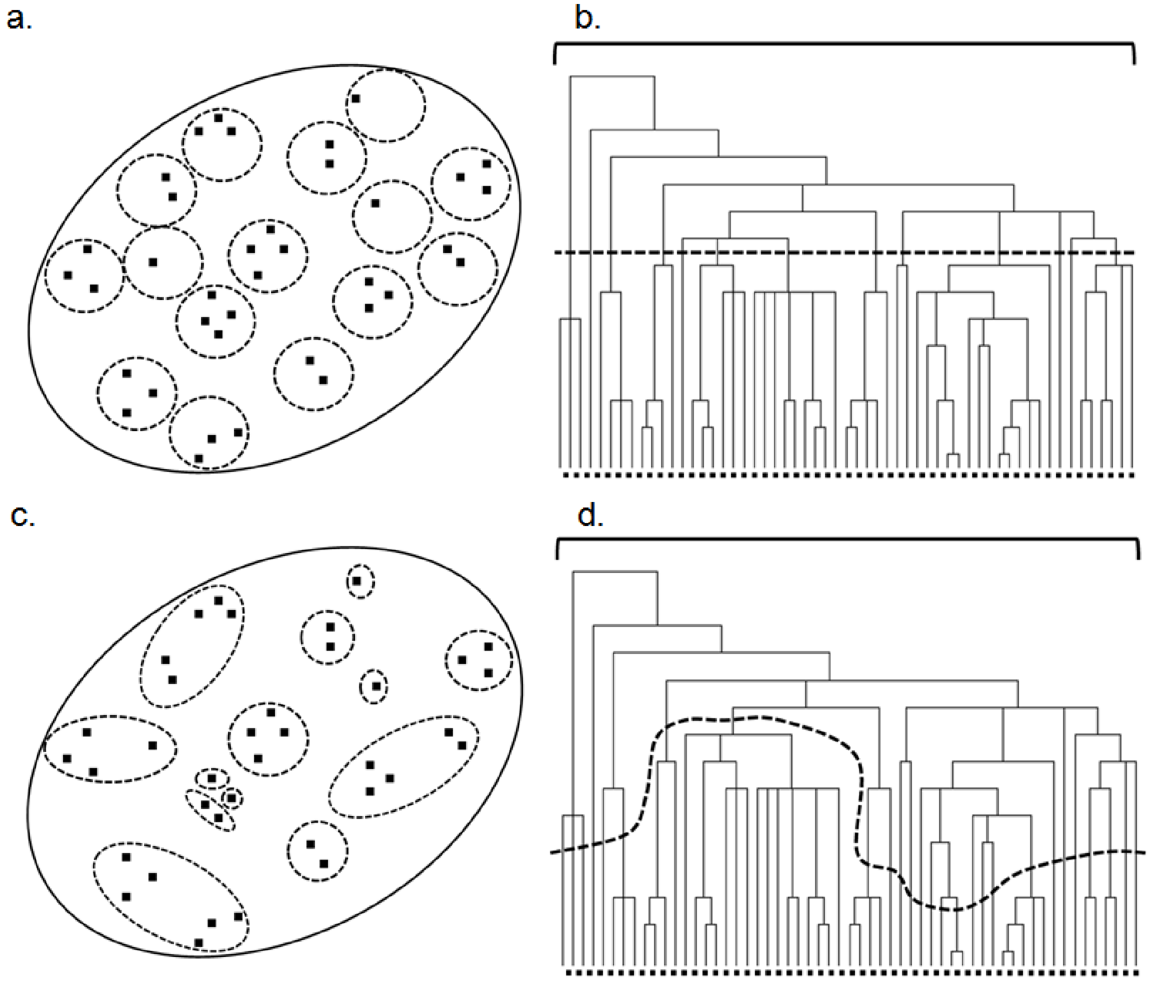


Figure 4.2. Conceptual parallels between spatial scale and phylogenetic scale of community studies: focus. Dashed lines show limits of refocused (aggregated) spatial sample units (left) or operational taxonomic units (right). Rigid focus is based on a uniform spatial distance (a) or phylogenetic distance (b). Flexible focus uses criteria other than distance to aggregate adjacent sample units (c) or operational taxonomic units (d).

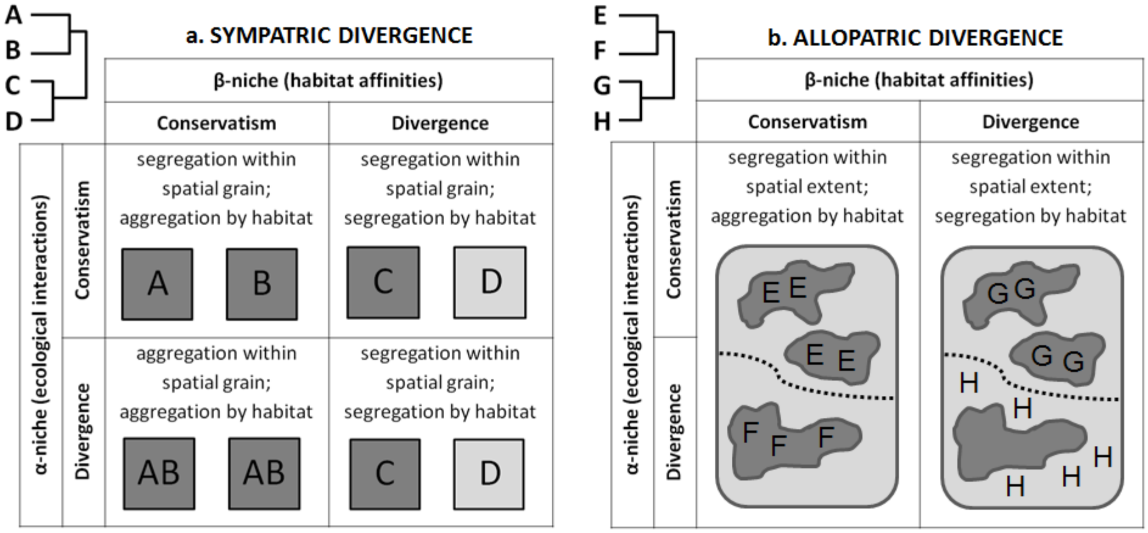


Figure 4.3. Conceptual model of expected aggregation and segregation patterns of closely related species under different scenarios of spatial and ecological divergence, building on Webb et al. (2002). Phylogenetic trees in upper left of a and b show relationships among hypothetical taxa whose expected spatial patterns are diagramed. a) Expected patterns of sympatric species within fine-grained sample units (squares) in different habitats (grayscale shades). b) Expected patterns of allopatric species within large spatial extents containing different habitats (grayscale shaded shapes). The dashed line represents a zone separating allopatric species ranges.

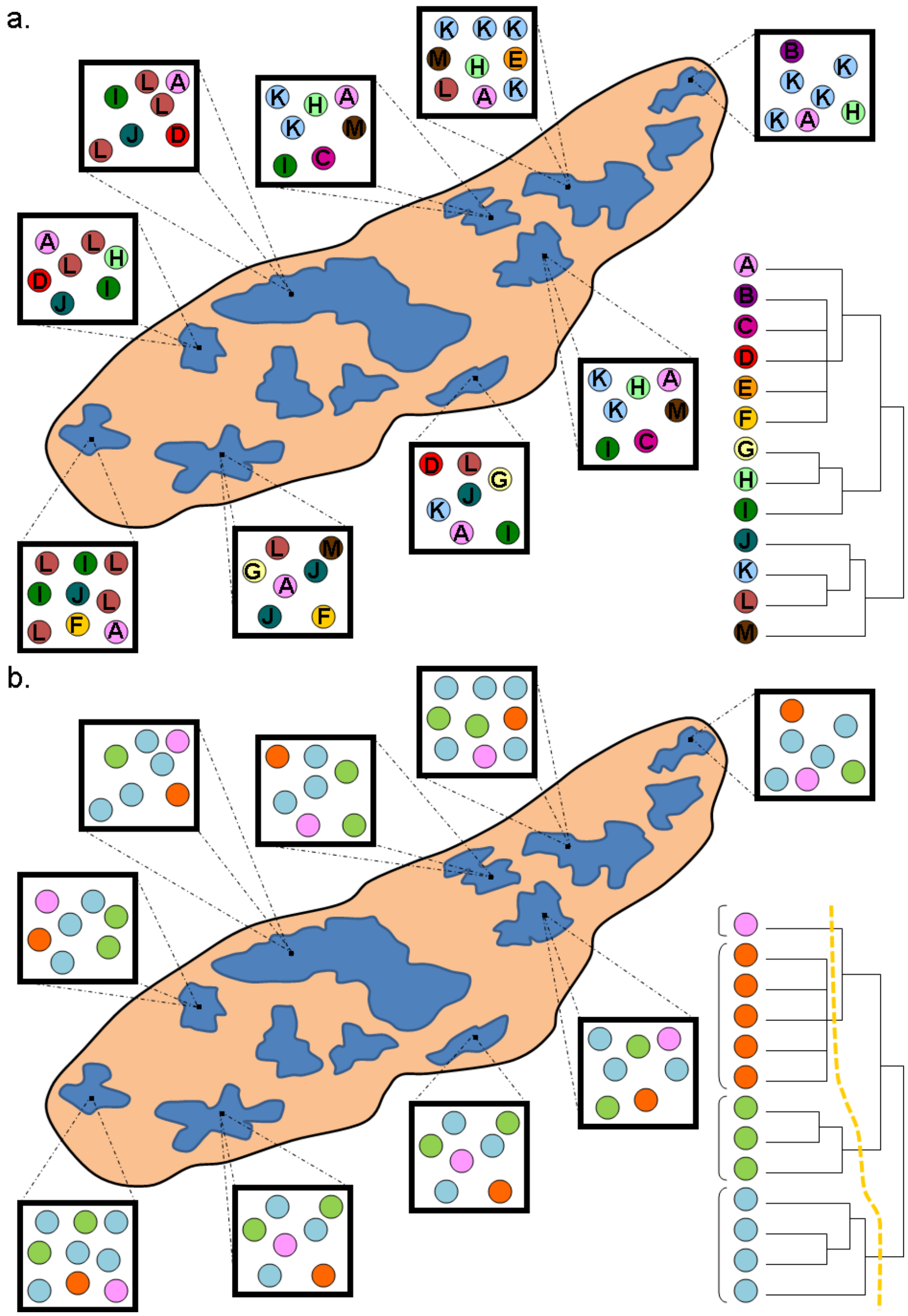
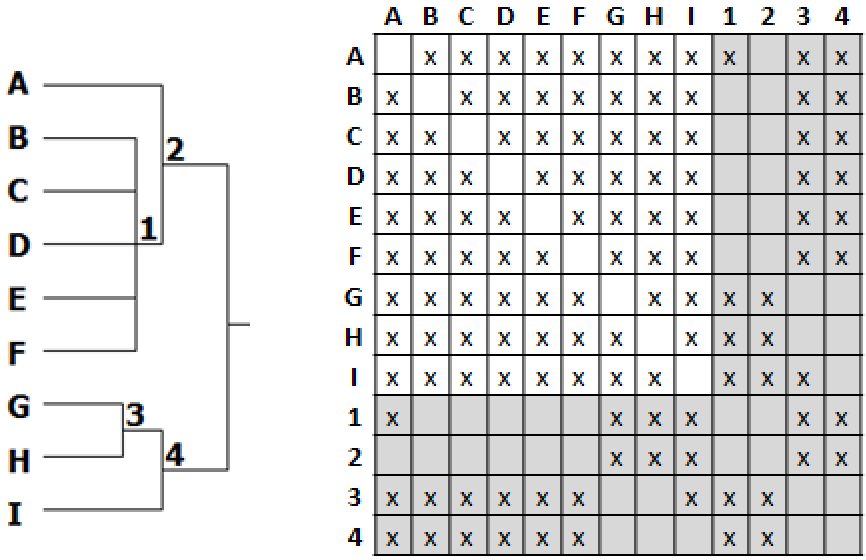


Figure 4.4. Hypothetical scenario illustrating phylogenetic refocusing of community patterns. a and b depict the same study area with different habitats shown in different colors (mimicking uplands and lowlands of the Southern Appalachian Region, USA). Squares are sample plots from different locations within the 'upland' habitat, containing taxa represented by letters/symbols, related according to phylogenetic models to the right. a) Species-level patterns with inconsistent composition in the 'upland' habitat. b) Phylogenetically-refocused pattern with consistent composition in the 'upland' habitat.



	A	B	C	D	E	F	G	H	I	1	2	3	4
A		x	x	x	x	x	x	x	x	x		x	x
B	x		x	x	x	x	x	x	x			x	x
C	x	x		x	x	x	x	x	x			x	x
D	x	x	x		x	x	x	x	x			x	x
E	x	x	x	x		x	x	x	x			x	x
F	x	x	x	x	x		x	x	x			x	x
G	x	x	x	x	x	x		x	x	x	x		
H	x	x	x	x	x	x	x		x	x	x		
I	x	x	x	x	x	x	x	x		x	x	x	
1	x						x	x	x			x	x
2							x	x	x			x	x
3	x	x	x	x	x	x			x	x	x		
4	x	x	x	x	x	x				x	x		

Figure 4.5. Expansion of a species by species pairwise association matrix to include higher taxa. Letters are species, numbers are higher taxa, related as shown in the phylogenetic tree (left). Shaded area of the full matrix (right) shows expansion due to inclusion of higher taxa. An "x" indicates taxon pairs that are phylogenetically independent (not overlapping members of the same lineage).

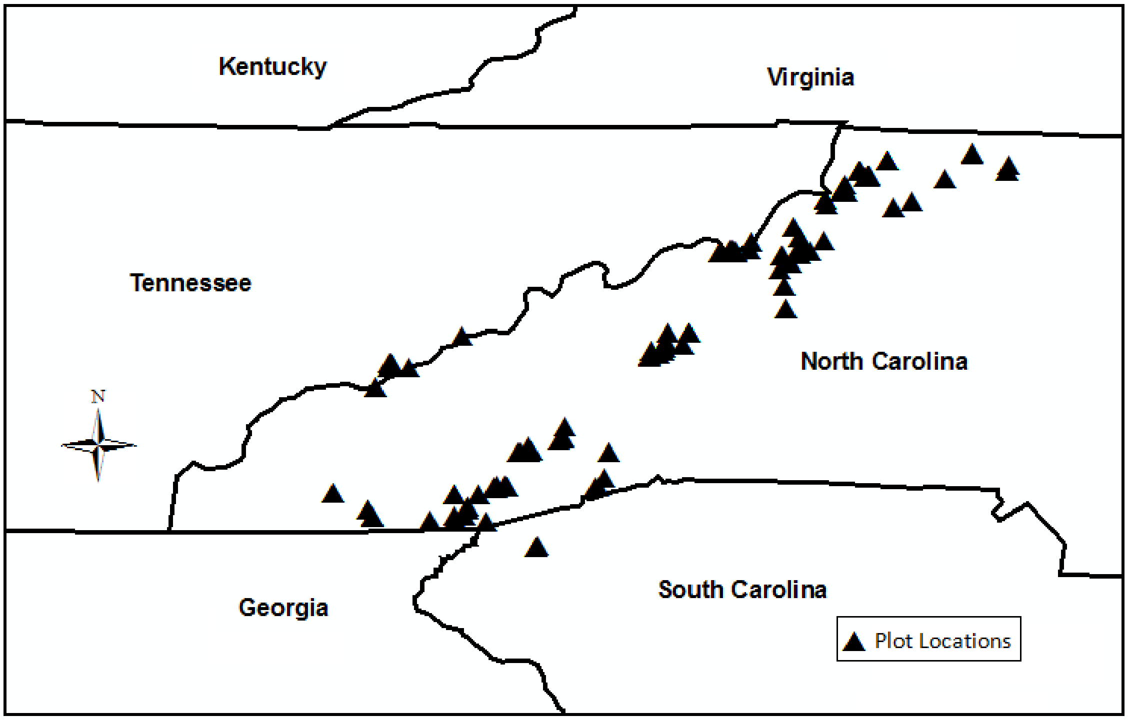


Figure 4.6. Location of high elevation rock outcrop and mountain bog vegetation survey plots in the Southern Appalachian Mountains, USA, analyzed using Multilevel Ordered Coalition Clustering (MOCC).

Table 4.1. Multilevel Coalition Clusters obtained by applying the MOCC algorithm to a plant community dataset of 219 100 m^2 vegetation plots taken from the Carolina Vegetation Survey, representing high elevation rock outcrops and mountain bogs.

Bog Cluster

Taxon	**Rank**
Acer rubrum	Species
Carex leptalea	Species
Clematis virginiana	Species
Drosera rotundifolia var. *rotundifolia*	Variety
Eleocharis	Subgenus
Eriophorum virginicum	Species
Eupatorium perfoliatum	Species
Galium	Genus
Glyceria	Genus
Impatiens	Genus
Juncus	Genus
Lycopus	Genus
Lyonia	Genus
Myrtales	Order
Orchidaceae	Family
Osmunda	Genus
Ovales	Section
Packera aurea	Species
Persicaria	Genus
Rhynchospora	Genus
Rosa	Genus
Rubus hispidus	Species
Salix sericea	Species
Scirpus	Genus
Solidago altissima var. *altissima*	Variety
Solidago patula	Species
Stellulatae	Section
Symphyotrichum puniceum	Species
Thelypteris	Genus
Trigynobrathys	Section
Vaccinium macrocarpon	Species
Vesicariae	Section
Viola	Genus

Rock Outcrop Cluster 1

Taxon	**Rank**
Andropogoneae	Tribe
Carex umbellata	Species
Danthonia sericea	Species
Dichanthelium	Genus
Houstonia longifolia	Species
Hypericum gentianoides	Species
Selaginella	Genus

Rock Outcrop Cluster 2

Taxon	**Rank**
Alnus viridis var. *crispa*	Variety
Deschampsia	Genus
Minuartia groenlandica	Species

General Bog + Rock Outcrop Cluster

Taxon	**Rank**
Cyanococcus	Section
Hymenanthes	Subgenus
Kalmia	Genus

APPENDIX 2.1

Taxa recorded by the 1999-2000 USGS-NPS vegetation survey of Zion National Park, Utah (Cogan et al. 2004), following nomenclature of Kartesz (1999), with translations to equivalent taxonomic concepts of the 1987-89 BYU-RMRS survey (Harper et al. 2001), updated to nomenclature of Welsh et al. (2003). USGS-NPS names are as they appear in the publicly-available database (USGS 2004); only taxa identified to species or genus are shown. Blanks in the BYU-RMRS column indicate taxa not recorded by the 1987-89 vegetation survey or (in the case of some genera) translating to multiple ecologically heterogeneous congeners. #Occ.=number of plot occurrences out of 346 (USGS-NPS) and 288 (BYU-RMRS) plots total.

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.	39	*Abies concolor*	19
Abronia fragrans Nutt. ex Hook.	4	*Abronia fragrans*	20
Acer grandidentatum Nutt.	35	*Acer grandidentatum*	29
Acer negundo L.	26	*Acer negundo*	18
Achillea millefolium L.	24	*Achillea millefolium*	6
Achnatherum contractum (B.L. Johnson) Barkworth	1	*Stipa hymenoides*	65
Achnatherum hymenoides (Roemer & J.A. Schultes) Barkworth	63	*Stipa hymenoides*	65
Achnatherum lettermanii (Vasey) Barkworth	12	*Stipa lettermanii*	12
Achnatherum nelsonii ssp. *nelsonii* (Scribn.) Barkworth	2	*Stipa nelsonii*	5
Achnatherum speciosum (Trin. & Rupr.) Barkworth	5	*Stipa speciosa*	15
Agastache urticifolia (Benth.) Kuntze	3	*Agastache urticifolia*	1
Agoseris Raf.	3		
Agropyron cristatum (L.) Gaertn.	3	*Agropyron cristatum*	1
Agrostis exarata Trin.	3	*Agrostis exarata*	3
Agrostis L.	2		
Agrostis stolonifera L.	4	*Agrostis stolonifera*	1
Allionia incarnata L.	1		
Allium L.	7		
Ambrosia acanthicarpa Hook.	1		
Amelanchier alnifolia (Nutt.) Nutt. ex M. Roemer	17	*Amelanchier alnifolia*	11
Amelanchier utahensis Koehne	139	*Amelanchier utahensis*	141
Andropogon gerardii Vitman	1	*Andropogon gerardii*	3
Antennaria dimorpha (Nutt.) Torr. & Gray	6		
Antennaria Gaertn.	8		
Apocynum androsaemifolium L.	1	*Apocynum androsaemifolium*	2
Aquilegia L.	2		
Arabis holboellii Hornem.	9		
Arabis L.	19	*Arabis hirsuta + perennans*	124
Arabis perennans S. Wats.	1	*Arabis perennans*	124
Arctostaphylos patula Greene	94	*Arctostaphylos patula*	94
Arctostaphylos pungens Kunth	12		
Arenaria fendleri Gray	26	*Arenaria fendleri*	23
Arenaria L.	3		
Arenaria macradenia S. Wats.	15	*Arenaria macradenia*	46

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Aristida purpurascens Poir.	2		
Aristida purpurea Nutt.	19	*Aristida purpurea*	26
Arnica L.	1		
Artemisia campestris L.	16	*Artemisia campestris*	14
Artemisia dracunculus L.	13	*Artemisia dracunculus*	12
Artemisia dracunculus ssp. *dracunculus* L.	1	*Artemisia dracunculus*	12
Artemisia filifolia Torr.	11	*Artemisia filifolia*	3
Artemisia ludoviciana Nutt.	52	*Artemisia ludoviciana*	51
Artemisia nova A. Nels.	24	*Artemisia arbuscula*	4
Artemisia tridentata Nutt.	70	*Artemisia tridentata*	55
Artemisia tridentata ssp. *tridentata* Nutt.	2	*Artemisia tridentata*	55
Artemisia tridentata ssp. *vaseyana* (Rydb.) Beetle	9	*Artemisia tridentata*	55
Asclepias subverticillata (Gray) Vail	2	*Asclepias subverticillata*	9
Asplenium L.	1		
Aster ascendens Lindl.	1		
Aster glaucodes Blake	1	*Aster glaucodes*	6
Aster L.	9		
Astragalus flavus Nutt.	2	*Astragalus flavus*	1
Astragalus L.	33		
Astragalus subcinereus Gray	2	*Astragalus subcinereus*	1
Atriplex canescens (Pursh) Nutt.	12	*Atriplex canescens*	10
Atriplex confertifolia (Torr. & Frem.) S. Wats.	2	*Atriplex confertifolia*	2
Atriplex L.	1		
Baccharis emoryi Gray	9	*Baccharis salicina*	3
Baccharis L.	2		
Baccharis salicifolia (Ruiz & Pavon) Pers.	4	*Baccharis salicina*	3
Baileya multiradiata Harvey & Gray ex Gray	1	*Baileya multiradiata*	8
Balsamorhiza sagittata (Pursh) Nutt.	10	*Balsamorhiza sagittata*	8
Betula occidentalis Hook.	7	*Betula occidentalis*	2
Bouteloua barbata Lag.	1		
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	34	*Bouteloua gracilis*	19
Bouteloua Lag.	1		
Brassica L.	1		
Brickellia atractyloides Gray	3		
Brickellia californica (Torr. & Gray) Gray	3	*Brickellia californica*	4
Brickellia Ell.	9		
Brickellia grandiflora (Hook.) Nutt.	5	*Brickellia grandiflora*	10
Brickellia longifolia S. Wats.	7		
Brickellia microphylla (Nutt.) Gray	2	*Brickellia microphylla*	5
Bromus anomalus Rupr. ex Fourn.	8	*Bromus anomalus*	5
Bromus diandrus Roth	16	*Bromus diandrus*	10
Bromus inermis Leyss.	14		
Bromus L.	3		
Bromus rubens L.	6	*Bromus rubens*	43
Bromus tectorum L.	99	*Bromus tectorum*	130
Calamagrostis Adans.	1	*Calamagrostis scopulorum*	1
Calochortus nuttallii Torr. & Gray	8	*Calochortus nuttallii*	23

USGS-NPS Name (Kartesz 1999)	**#Occ**	**BYU-RMRS Name (Welsh et al. 2003)**	**#Occ**
Calochortus Pursh	3		
Carex geyeri Boott	2	*Carex* sp.	7
Carex L.	19	*Carex* sp.+*aurea*+*hystericina*+*occidentalis*+*rossii*	75
Carex L. (*occidentalis*?)	1	*Carex occidentalis*	1
Carex L. (*rossii*?)	1	*Carex rossii*	67
Carex microptera Mackenzie	5	*Carex* sp.	7
Carex nebrascensis Dewey	2	*Carex* sp.	7
Carex occidentalis Bailey	8	*Carex occidentalis*	1
Carex rossii Boott	11	*Carex rossii*	67
Carex utriculata Boott	2	*Carex* sp.	7
Castilleja applegatei ssp. *martinii* (Abrams) Chuang & Heckard	3	*Castilleja chromosa*	2
Castilleja flava var. *flava* S. Wats.	1		
Castilleja linariifolia Benth.	8	*Castilleja linariifolia*	7
Castilleja Mutis ex L. f.	8		
Ceanothus fendleri Gray	5		
Ceanothus L.	1		
Ceanothus martinii M.E. Jones	2	*Ceanothus martinii*	4
Celtis laevigata var. *reticulata* (Torr.) L. Benson	6	*Celtis reticulata*	2
Cenchrus longispinus (Hack.) Fern.	1	*Cenchrus longispinus*	2
Cercocarpus intricatus S. Wats.	23	*Cercocarpus intricatus*	40
Cercocarpus ledifolius Nutt.	2		
Cercocarpus montanus Raf.	46	*Cercocarpus montanus*	33
Chaenactis DC.	2	*Chaenactis douglasii*+*stevioides*	45
Chaenactis DC. (*douglasii* or *stevioides*??)	1	*Chaenactis douglasii*+*stevioides*	45
Chaenactis douglasii (Hook.) Hook. & Arn.	9	*Chaenactis douglasii*	44
Chaenactis stevioides Hook. & Arn.	1	*Chaenactis stevioides*	1
Chaetopappa ericoides (Torr.) Nesom	2	*Chaetopappa ericoides*	1
Chamaesyce albomarginata (Torr. & Gray) Small	1	*Chamaesyce albomarginata*	23
Chamaesyce fendleri (Torr. & Gray) Small	8	*Chamaesyce fendleri*	3
Chamaesyce glyptosperma (Engelm.) Small	4		
Chamaesyce parryi (Engelm.) Rydb.	1		
Chenopodium album L.	2		
Chenopodium fremontii S. Wats.	4	*Chenopodium fremontii*	3
Chenopodium L.	1		
Chimaphila umbellata (L.) W. Bart.	1	*Chimaphila umbellata*	1
Chrysothamnus depressus Nutt.	3	*Chrysothamnus depressus*	5
Chrysothamnus Nutt.	1		
Chrysothamnus viscidiflorus (Hook.) Nutt.	15	*Chrysothamnus viscidiflorus*	6
Chrysothamnus viscidiflorus ssp. *axillaris* (Keck) L.C. Anders.	1	*Chrysothamnus viscidiflorus*	6
Cirsium arizonicum (Gray) Petrak	1	*Cirsium arizonicum*	16
Cirsium calcareum (M.E. Jones) Woot. & Standl.	2		
Cirsium P. Mill.	18		
Cirsium vulgare (Savi) Ten.	1		
Cirsium wheeleri (Gray) Petrak	7	*Cirsium wheeleri*	8
Claytonia perfoliata ssp. *perfoliata* var. *nubigena* (Greene) Poelln.	4	*Montia perfoliata*	3
Clematis columbiana (Nutt.) Torr. & Gray	2	*Clematis columbiana*	3
Clematis L.	1		

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Clematis ligusticifolia Nutt.	9		
Coleogyne ramosissima Torr.	12	*Coleogyne ramosissima*	13
Collinsia parviflora Lindl.	1	*Collinsia parviflora*	2
Comandra umbellata (L.) Nutt.	38	*Comandra umbellata*	35
Comandra umbellata ssp. *pallida* (A. DC.) Piehl	3	*Comandra umbellata*	35
Convolvulus arvensis L.	2	*Convolvulus arvensis*	1
Cordylanthus kingii S. Wats.	2	*Cordylanthus kingii*	19
Cordylanthus parviflorus (Ferris) Wiggins	4		
Crepis intermedia Gray	1		
Cryptantha humilis (Gray) Payson	2	*Cryptantha humilis*	1
Cryptantha Lehm. ex G. Don	15		
Cupressus arizonica Greene	1		
Dactylis glomerata L.	3	*Dactylis glomerata*	2
Dalea searlsiae (Gray) Barneby	3	*Dalea searlsiae*	13
Datura L.	1		
Datura wrightii Regel	5	*Datura wrightii*	3
Descurainia pinnata (Walt.) Britt.	1	*Descurainia pinnata*	28
Descurainia Webb & Berth.	1		
Distichlis spicata (L.) Greene	1	*Distichlis spicata*	1
Draba L.	4		
Dracocephalum parviflorum Nutt.	1	*Dracocephalum parviflorum*	1
Echinocereus Engelm.	3		
Echinocereus engelmannii (Parry ex Engelm.) Lem.	9	*Echinocereus engelmannii*	7
Echinocereus triglochidiatus Engelm.	11	*Echinocereus triglochidiatus*	22
Elaeagnus angustifolia L.	4		
Eleocharis R. Br.	1		
Elymus canadensis L.	3	*Elymus canadensis*	4
Elymus elymoides (Raf.) Swezey	59	*Elymus elymoides*	58
Elymus elymoides ssp. *elymoides* (Raf.) Swezey	1	*Elymus elymoides*	58
Elymus glaucus Buckl.	1		
Elymus L.	10		
Elymus lanceolatus (Scribn. & J.G. Sm.) Gould	11	*Elymus smithii*	3
Elytrigia intermedia (Host) Nevski	2	*Elymus hispidus*	1
Elytrigia intermedia ssp. *intermedia* (Host) Nevski	1	*Elymus hispidus*	1
Elytrigia repens (L.) Desv. ex B.D. Jackson	6		
Ephedra nevadensis	1	*Ephedra nevadensis*	18
Ephedra nevadensis S. Wats.	18	*Ephedra nevadensis*	18
Ephedra viridis Coville	25	*Ephedra viridis*	16
Epilobium brachycarpum K. Presl	7	*Epilobium brachycarpum*	3
Epilobium canum ssp. *garrettii* (A. Nels.) Raven	1	*Zauschneria latifolia*	15
Epilobium canum ssp. *latifolium* (Hook.) Raven	3	*Zauschneria latifolia*	15
Equisetum arvense L.	6	*Equisetum arvense*	1
Equisetum hyemale L.	3	*Equisetum hyemale*	8
Equisetum L.	3	*Equisetum arvense+hymenale+laevigatum*	8
Equisetum laevigatum A. Braun	6	*Equisetum laevigatum*	2
Equisetum variegatum Schleich. ex F. Weber & D.M.H. Mohr	4		
Ericameria linearifolia (DC.) Urbatsch & Wussow	4		

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Ericameria nauseosa ssp. *nauseosa* var. *nauseosa*	43	*Chrysothamnus nauseosus*	39
Ericameria parryi var. *parryi* (Gray) Nesom	1	*Chrysothamnus parryi*	1
Erigeron argentatus Gray	1		
Erigeron concinnus var. *concinnus* (Hook. & Arn.) Torr. & Gray	1	*Erigeron pumilus*	1
Erigeron divergens Torr. & Gray	2	*Erigeron divergens*	17
Erigeron L.	37		
Erigeron pumilus Nutt.	1	*Erigeron pumilus*	1
Erigeron speciosus (Lindl.) DC.	2	*Erigeron speciosus*	6
Erigeron speciosus var. *macranthus* (Nutt.) Cronq.	1	*Erigeron speciosus*	6
Erigeron utahensis Gray	6	*Erigeron utahensis*	41
Eriogonum corymbosum Benth.	1	*Eriogonum corymbosum*	1
Eriogonum fasciculatum Benth.	1	*Eriogonum fasciculatum*	3
Eriogonum flavum Nutt.	1		
Eriogonum inflatum Torr. & Frem.	3	*Eriogonum inflatum*	3
Eriogonum Michx.	23		
Eriogonum microthecum Nutt.	5	*Eriogonum microthecum*	15
Eriogonum ovalifolium Nutt.	1		
Eriogonum panguicense (M.E. Jones) Reveal	2		
Eriogonum racemosum Nutt.	21	*Eriogonum racemosum*	59
Eriogonum umbellatum Torr.	27	*Eriogonum umbellatum*	21
*Eriogonum*2 Michx.	2		
Erioneuron pulchellum (Kunth) Tateoka	1		
Erodium cicutarium (L.) L'Her. ex Ait.	6	*Erodium cicutarium*	10
Erysimum capitatum var. *argillosum* (Greene) R.J. Davis	8	*Erysimum asperum*	64
Erysimum capitatum var. *capitatum* (Dougl. ex Hook.) Greene	1	*Erysimum asperum*	64
Euphorbia brachycera Engelm.	1	*Euphorbia brachycera*	5
Euphorbia L.	14		
Fendlerella utahensis (S. Wats.) Heller	2	*Fendlerella utahensis*	1
Festuca L.	2		
Festuca occidentalis Hook.	1		
Frasera speciosa Dougl. ex Griseb.	11	*Swertia radiate*	11
Fraxinus anomala Torr. ex S. Wats.	34	*Fraxinus anomala*	45
Fraxinus velutina Torr.	9	*Fraxinus velutina*	6
Gaillardia Foug.	1		
Galium aparine L.	1	*Galium aparine*	6
Galium L.	6		
Gayophytum A. Juss.	1	*Gayophytum* sp.	14
Geraea canescens Torr. & Gray	1		
Geranium caespitosum James	1		
Geranium L.	1		
Gilia Ruiz & Pavon	1		
Grayia spinosa (Hook.) Moq.	2		
Grindelia squarrosa (Pursh) Dunal	1	*Grindelia squarrosa*	1
Gutierrezia microcephala (DC.) Gray	21	*Gutierrezia* sp.	94
Gutierrezia sarothrae (Pursh) Britt. & Rusby	81	*Gutierrezia* sp.	94
Helianthella uniflora (Nutt.) Torr. & Gray	5		
Helianthus petiolaris Nutt.	3		

USGS-NPS Name (Kartesz 1999)	**#Occ**	**BYU-RMRS Name (Welsh et al. 2003)**	**#Occ**
Heliomeris multiflora var. *multiflora* Nutt.	9	*Viguiera multiflora*	12
Hesperodoria scopularum (M.E. Jones) Greene	3	*Haplopappus scopulorum*	42
Hesperostipa comata ssp. *comata* (Trin. & Rupr.) Barkworth	34	*Stipa comata*	39
Heterotheca villosa (Pursh) Shinners	69	*Chrysopsis villosa*	74
Heterotheca viscida (Gray) Harms	1	*Chrysopsis villosa*	74
Heuchera rubescens Torr.	1	*Heuchera rubescens*	12
Heuchera rubescens var. *versicolor* (Greene) M.G. Stewart	2	*Heuchera rubescens*	12
Holodiscus dumosus (Nutt. ex Hook.) Heller	2	*Holodiscus dumosus*	21
Hordeum brachyantherum Nevski	1		
Hydrophyllum occidentale (S. Wats.) Gray	3	*Hydrophyllum occidentale*	2
Hymenopappus filifolius Hook.	22	*Hymenopappus filifolius*	11
Hymenopappus L'Her.	1	*Hymenopappus filifolius*	11
Hypochaeris radicata L.	1		
Ipomoea purpurea (L.) Roth	1		
Ipomopsis aggregata (Pursh) V. Grant	3	*Ipomopsis aggregate*	5
Ipomopsis arizonica (Greene) Wherry	1	*Ipomopsis aggregata*	5
Ipomopsis congesta ssp. *congesta* (Hook.) V. Grant	5	*Ipomopsis congesta*	14
Ipomopsis congesta ssp. *frutescens* (Rydb.) Day	1	*Ipomopsis congesta*	14
Ivesia sabulosa (M.E. Jones) Keck	3	*Ivesia sabulosa*	7
Juncus balticus Willd.	6	*Juncus arcticus*	3
Juncus ensifolius Wikstr.	2	*Juncus ensifolius*	2
Juncus L.	3	*Juncus arcticus+ensifolius+tenuis*	4
Juncus longistylis Torr.	3		
Juncus tenuis Willd.	3	*Juncus tenuis*	1
Juncus torreyi Coville	1		
Juniperus L.	1		
Juniperus osteosperma (Torr.) Little	119	*Juniperus osteosperma*	115
Juniperus scopulorum Sarg.	50	*Juniperus scopulorum*	21
Kelloggia galioides Torr.	4		
Koeleria macrantha (Ledeb.) J.A. Schultes	6	*Koeleria macrantha*	1
Krameria L.	1		
Lactuca L.	3		
Lactuca serriola L.	3	*Lactuca serriola*	13
Lathyrus brachycalyx Rydb.	1	*Lathyrus brachycalyx*	9
Lathyrus L.	3		
Lathyrus L. ? *Vicia*?	1		
Lepidium L.	3		
Leptodactylon pungens (Torr.) Torr. ex Nutt.	1	*Leptodactylon pungens*	8
Leptodactylon watsonii (Gray) Rydb.	1	*Leptodactylon watsonii*	10
Lesquerella S. Wats.	1		
Leymus cinereus (Scribn. & Merr.) A. Love	1		
Linanthus nuttallii ssp. *nuttallii* (Gray) Greene ex Milliken	1	*Linanthastrum nuttallii*	19
Linaria dalmatica (L.) P. Mill.	2		
Linum L.	4		
Linum perenne L.	4	*Linum perenne*	6
Lomatium graveolens (S. Wats.) Dorn & Hartman	1	*Lomatium graveolens*	1
Lomatium Raf.	3		

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Lotus L.	5		
Lotus rigidus (Benth.) Greene	2		
Lotus utahensis Ottley	26	*Lotus utahensis*	12
Lupidium species	1		
Lupinus argenteus Pursh	15	*Lupinus argenteus*	1
Lupinus concinnus J.G. Agardh	1	*Lupinus concinnus*	1
Lupinus L.	18		
Lupinus sericeus Pursh	3	*Lupinus sericeus*	9
Luzula campestris (L.) DC.	1		
Luzula parviflora (Ehrh.) Desv.	4		
Lycium L.	1		
Lycium pallidum Miers	4	*Lycium pallidum*	3
Lygodesmia grandiflora (Nutt.) Torr. & Gray	1	*Lygodesmia grandiflora*	2
Lygodesmia juncea (Pursh) D. Don ex Hook.	1		
Machaeranthera canescens (Pursh) Gray	21	*Machaeranthera canescens*	40
Machaeranthera gracilis (Nutt.) Shinners	2	*Haplopappus gracilis*	4
Machaeranthera Nees	6		
Mahonia repens (Lindl.) G. Don	40	*Mahonia repens*	29
Maianthemum racemosum ssp. *racemosum* (L.) Link	6	*Smilacina racemosa*	6
Maianthemum stellatum (L.) Link	9	*Smilacina stellata*	3
Medicago lupulina L.	2	*Medicago lupulina*	1
Melilotus officinalis (L.) Lam.	16	*Melilotus officinalis*	1
Mentha arvensis L.	3		
Mentha X piperita L. (pro sp.)	1		
Mertensia arizonica Greene	10	*Mertensia arizonica*	7
Mertensia Roth	3		
Mirabilis multiflora (Torr.) Gray	3	*Mirabilis multiflora*	7
Monardella odoratissima Benth.	1	*Monardella odoratissima*	6
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi	3	*Muhlenbergia asperifolia*	2
Muhlenbergia montana (Nutt.) A.S. Hitchc.	8	*Muhlenbergia montana*	2
Muhlenbergia pauciflora Buckl.	1		
Muhlenbergia porteri Scribn. ex Beal	3		
Muhlenbergia racemosa (Michx.) B.S.P.	2	*Muhlenbergia racemosa*	3
Muhlenbergia Schreb.	5		
Muhlenbergia thurberi Rydb.	1	*Muhlenbergia thurberi*	12
Muhlenbergia wrightii Vasey ex Coult.	1		
Nassella viridula (Trin.) Barkworth	2		
Nicotiana attenuata Torr. ex S. Wats.	1	*Nicotiana attenuata*	1
Oenothera cespitosa Nutt.	1	*Oenothera caespitosa*	9
Oenothera flava (A. Nels.) Garrett	1		
Oenothera howardii (A. Nels.) W.L. Wagner	1		
Oenothera L.	8		
Oenothera longissima Rydb.	1	*Oenothera longissima*	2
Oenothera pallida Lindl.	6	*Oenothera pallida*	12
Opuntia basilaris Engelm. & Bigelow	9		
Opuntia chlorotica Engelm. & Bigelow	3		
Opuntia echinocarpa Engelm. & Bigelow	2		

USGS-NPS Name (Kartesz 1999)	**#Occ**	**BYU-RMRS Name (Welsh et al. 2003)**	**#Occ**
Opuntia engelmannii Salm-Dyck	1	*Opuntia phaeacantha*	9
Opuntia erinacea Engelm. & Bigelow ex Engelm.	5	*Opuntia erinacea*	17
Opuntia macrorhiza Engelm.	103	*Opuntia macrorhiza*	120
Opuntia P. Mill.	4		
Opuntia phaeacantha Engelm.	36	*Opuntia phaeacantha*	9
Opuntia polyacantha Haw.	4	*Opuntia polyacantha*	3
Opuntia whipplei Engelm. & Bigelow	6	*Opuntia whipplei*	3
Osmorhiza depauperata Phil.	2		
Osmorhiza occidentalis (Nutt. ex Torr. & Gray) Torr.	6	*Osmorhiza occidentalis*	4
Osmorhiza Raf.	1		
Oxytropis DC.	1		
Pascopyrum smithii (Rydb.) A. Love	10	*Elymus smithii*	3
Paxistima myrsinites (Pursh) Raf.	39	*Pachystima myrsinites*	54
Penstemon caespitosus Nutt. ex Gray	10		
Penstemon comarrhenus Gray	1	*Penstemon comarrhenus*	2
Penstemon eatonii Gray	14	*Penstemon eatonii*	23
Penstemon humilis Nutt. ex Gray	3	*Penstemon humilis*	27
Penstemon lentus Pennell	1		
Penstemon leonardii Rydb.	6	*Penstemon higginsii*	5
Penstemon leonardii var. *higginsii* Neese	1	*Penstemon higginsii*	5
Penstemon linarioides Gray	9	*Penstemon linarioides*	13
Penstemon pachyphyllus Gray ex Rydb.	2	*Penstemon pachyphyllus*	1
Penstemon palmeri Gray	16	*Penstemon palmeri*	19
Penstemon rostriflorus Kellogg	2	*Penstemon rostriflorus*	30
Penstemon Schmidel	38		
Penstemon tusharensis N. Holmgren	1		
Peraphyllum ramosissimum Nutt.	10	*Peraphyllum ramosissimum*	10
Petradoria pumila (Nutt.) Greene	7	*Petradoria pumila*	2
Petrophyton caespitosum (Nutt.) Rydb.	3	*Petrophytum caespitosum*	12
Phacelia heterophylla Pursh	21	*Phacelia heterophylla*	42
Phacelia Juss.	5		
Phleum pratense L.	1		
Phlox austromontana Coville	32	*Phlox austromontana*	54
Phlox caespitosa Nutt.	1		
Phlox hoodii Richards.	6		
Phlox L.	7		
Phlox longifolia Nutt.	1	*Phlox longifolia*	11
Phoradendron juniperinum Engelm.	2	*Phoradendron juniperinum*	14
Phragmites australis (Cav.) Trin. ex Steud.	1	*Phragmites australis*	2
Physalis hederifolia Gray	1	*Physalis hederifolia*	8
Physalis heterophylla Nees	1		
Physaria (Nutt. ex Torr. & Gray) Gray	2		
Physaria chambersii Rollins	6	*Physaria chambersii*	3
Physaria newberryi Gray	1	*Physaria newberryi*	7
Pinus edulis Engelm.	48	*Pinus edulis*	53
Pinus edulis x monophylla Engelm.	4	*Pinus edulis+monophylla*	115
Pinus monophylla Torr. & Frem.	58	*Pinus monophylla*	64

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Pinus ponderosa P.& C. Lawson	74	*Pinus ponderosa*	60
Plagiobothrys tenellus (Nutt. ex Hook.) Gray	1		
Plantago patagonica Jacq.	3	*Plantago patagonica*	13
Pleuraphis jamesii Torr.	26	*Hilaria* sp.	41
Pluchea sericea (Nutt.) Coville	2		
Poa fendleriana (Steud.) Vasey	155	*Poa fendleriana*	190
Poa L.	4		
Poa pratensis L.	44	*Poa pratensis*	14
Poa secunda J. Presl	14	*Poa secunda*	4
*Poa*2 L.	1		
Polygonum douglasii Greene	8	*Polygonum douglasii*	39
Polygonum L.	3		
Polypodium hesperium Maxon	1	*Polypodium hesperium*	6
Polypogon Desf.	1		
Populus angustifolia James	1		
Populus fremontii S. Wats.	22	*Populus fremontii*	6
Populus tremuloides Michx.	11	*Populus tremuloides*	2
Potentilla glandulosa Lindl.	1		
Prosopis glandulosa Torr.	1		
Prunus L.	1		
Prunus virginiana L.	14	*Prunus virginiana*	10
Pseudoroegneria spicata ssp. *spicata* (Pursh) A. Love	1	*Elymus spicatus*	6
Pseudostellaria jamesiana (Torr.) W.A. Weber & R.L. Hartman	3	*Stellaria jamesiana*	18
Pseudotsuga menziesii (Mirbel) Franco	19	*Pseudotsuga menziesii*	18
Psoralidium Rydb.	1		
Psorothamnus fremontii (Torr. ex Gray) Barneby	8	*Psorothamnus fremontii*	11
Psorothamnus fremontii var. *fremontii* (Torr. ex Gray) Barneby	1	*Psorothamnus fremontii*	11
Pteridium aquilinum (L.) Kuhn	4	*Pteridium aquilinum*	3
Pterospora andromedea Nutt.	1	*Pterospora andromedea*	2
Puccinellia distans (Jacq.) Parl.	1		
Purshia DC. ex Poir.	1		
Purshia mexicana (D. Don) Henrickson	11	*Purshia mexicana*	15
Purshia stansburiana (Torr.) Henrickson	6	*Purshia mexicana*	15
Purshia tridentata (Pursh) DC.	51	*Purshia tridentata*	36
Quercus gambelii Nutt.	166	*Quercus gambelii*	135
Quercus turbinella Greene	40	*Quercus turbinella*	50
Rhus aromatica Ait.	9	*Rhus aromatica*	23
Rhus trilobata Nutt.	16	*Rhus aromatica*	23
Rhus trilobata var. *trilobata* Nutt.	10	*Rhus aromatica*	23
Rorippa nasturtium-aquaticum (L.) Hayek	1	*Nasturtium officinale*	1
Rosa woodsii Lindl.	19	*Rosa woodsii*	12
Rumex acetosella L.	2		
Rumex hymenosepalus Torr.	2	*Rumex hymenosepalus*	2
Salix exigua Nutt.	12	*Salix exigua*	3
Salix gooddingii Ball	2		
Salix L.	4		
Salix lasiolepis Benth.	1		

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Salix ligulifolia (Ball) Ball ex Schneid.	1		
Salix lucida Muhl.	1		
Salix lucida ssp. *lasiandra* (Benth.) E. Murr.	1		
Salix scouleriana Barratt ex Hook.	2	*Salix scouleriana*	2
Salsola kali ssp. *tragus* (L.) Celak.	1		
Salvia dorrii (Kellogg) Abrams	5	*Salvia dorrii*	3
Sambucus L.	1		
Schizachyrium scoparium (Michx.) Nash	2		
Schoenoplectus americanus (Pers.) Volk. ex Schinz & R. Keller	1		
Schoenoplectus tabernaemontani (K.C. Gmel.) Palla	1		
Scirpus L.	1		
Senecio eremophilus Richards.	3	*Senecio eremophilus*	3
Senecio integerrimus Nutt.	1		
Senecio L.	14		
Senecio multilobatus Torr. & Gray ex Gray	31	*Senecio multilobatus*	99
Senecio spartioides Torr. & Gray	19	*Senecio spartioides*	26
Shepherdia rotundifolia Parry	12	*Shepherdia rotundifolia*	17
Sisymbrium altissimum L.	3	*Sisymbrium altissimum*	4
Sisymbrium L.	1	*Sisymbrium altissimum+irio*	6
Sisyrinchium demissum Greene	2		
skeletonweed	1		
Solanum elaeagnifolium Cav.	1		
Solidago L.	1		
Solidago velutina DC.	9	*Solidago velutina*	38
Sorghastrum nutans (L.) Nash	2		
Sphaeralcea ambigua Gray	2	*Sphaeralcea ambigua*	2
Sphaeralcea coccinea (Nutt.) Rydb.	12		
Sphaeralcea grossulariifolia (Hook. & Arn.) Rydb.	4	*Sphaeralcea grossulariifolia*	14
Sphaeralcea St.-Hil.	6		
Sphaeromeria ruthiae Holmgren, Shultz & Lowrey	2	*Sphaeromeria ruthiae*	3
Sporobolus cryptandrus (Torr.) Gray	60	*Sporobolus cryptandrus*	50
Sporobolus R. Br.	1		
Stanleya pinnata (Pursh) Britt.	3	*Stanleya pinnata*	2
Stellaria L.	2		
Stellaria media (L.) Vill.	2		
Stephanomeria exigua Nutt.	1	*Stephanomeria exigua*	1
Stephanomeria Nutt.	2		
Stephanomeria tenuifolia (Raf.) Hall	1	*Stephanomeria tenuifolia*	51
Stipa L.	6		
Stipa L. (comata or lettermanii)	1		
Streptanthus cordatus Nutt.	3	*Streptanthus cordatus*	38
Symphoricarpos longiflorus Gray	4		
Symphoricarpos oreophilus Gray	79	*Symphoricarpos oreophilus*	58
Tamarix ramosissima Ledeb.	10	*Tamarix chinensis*	5
Taraxacum officinale G.H. Weber ex Wiggers	7	*Taraxacum officinale*	11
Tetradymia axillaris A. Nels.	1		
Tetradymia canescens DC.	10	*Tetradymia canescens*	9

USGS-NPS Name (Kartesz 1999)	#Occ	BYU-RMRS Name (Welsh et al. 2003)	#Occ
Thalictrum fendleri Engelm. ex Gray	15	*Thalictrum fendleri*	12
Thalictrum L.	1		
Thermopsis montana Nutt.	2	*Thermopsis montana*	4
Townsendia Hook.	2		
Toxicodendron rydbergii (Small ex Rydb.) Greene	2	*Toxicodendron rydbergii*	2
Tradescantia occidentalis (Britt.) Smyth	14	*Tradescantia occidentalis*	22
Tragia ramosa Torr.	1		
Tragopogon dubius Scop.	22	*Tragopogon dubius*	8
Tribulus terrestris L.	2	*Tribulus terrestris*	2
Trifolium gymnocarpon Nutt.	1		
Trifolium L.	3		
Trifolium longipes Nutt.	3	*Trifolium longipes*	10
Triticum aestivum L.	1		
Typha angustifolia L.	2	*Typha latifolia*	1
Typha domingensis Pers.	1	*Typha latifolia*	1
Verbascum thapsus L.	14	*Verbascum thapsus*	5
Verbena bracteata Lag. & Rodr.	3		
Vicia americana Muhl. ex Willd.	50	*Vicia americana*	43
Vicia L.	5		
Viola charlestonensis M.S. Baker & J.C. Clausen ex Clokey	1	*Viola purpurea*	10
Viola L.	1		
Vitis arizonica Engelm.	4	*Vitis arizonica*	1
Vulpia octoflora var. *octoflora* (Walt.) Rydb.	4	*Festuca octoflora*	74
Wyethia arizonica Gray	2	*Wyethia arizonica*	5
Yucca baccata Torr.	20	*Yucca baccata*	17
Yucca elata var. *utahensis* (McKelvey) Reveal	79	*Yucca angustissima*	41

APPENDIX 2.2

Vascular plant species/taxa recorded by the 1987-89 vegetation survey of Zion National Park, Utah (Harper 1993), and their affinities to coalition species groups. #Occ.=number of plot occurrences out of 288 plots total. Affinities are mean pairwise association values (in units of the phi coefficient) between a species and members of a coalition group (see also Table 2.2). Green and red shadings for low and high affinity values, respectively, are scaled separately for each column. Nomenclature follows Welsh et al. (2003) and names are cross-walked with Cogan et al. (2004) and Alexander and Fertig (2009) (see footnotes).

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Abies concolor	Pinaceae	19	-0.0226	-0.0893	-0.0770	-0.0559	0.0865	0.0603	0.0229	0.1859	0.2236	0.0410
Abronia fragrans	Nyctaginaceae	20	-0.0448	-0.0051	0.0253	0.2521	0.0395	-0.0448	-0.0382	-0.0325	-0.0349	-0.0360
*Acer glabrum**	Aceraceae	6	-0.0269	-0.0484	-0.0117	-0.0307	0.1020	0.0035	-0.0116	0.0185	0.1461	0.0090
Acer grandidentatum	Aceraceae	29	-0.0556	-0.0988	-0.0451	-0.0489	0.0587	0.0312	0.0003	0.1139	0.2614	0.0429
Acer negundo	Aceraceae	18	-0.0226	-0.0711	-0.0929	-0.0678	0.0736	-0.0447	-0.0579	0.0499	0.3163	0.2513
Achillea millefolium	Compositae	6	-0.0003	-0.0443	-0.0386	0.0190	0.0046	-0.0178	0.0136	0.2048	0.0272	0.0380
*Actaea rubra**	Ranunculaceae	2	-0.0154	-0.0290	-0.0467	-0.0189	0.0224	0.0006	-0.0186	0.0479	0.2531	0.0817
*Adiantum capillus-veneris**	Polypodiaceae	2	-0.0154	-0.0290	-0.0466	-0.0340	-0.0028	-0.0352	-0.0308	0.0132	0.1540	-0.0025
*Adiantum pedatum**	Polypodiaceae	1	-0.0109	-0.0204	-0.0291	-0.0027	0.0370	0.0140	-0.0138	0.0581	0.2611	0.1104
Agastache urticifolia	Labiatae	1	-0.0109	-0.0133	-0.0368	-0.0149	-0.0163	-0.0150	-0.0040	0.2240	-0.0098	0.0533
*Agoseris aurantiaca**	Compositae	1	-0.0109	-0.0071	-0.0067	-0.0149	-0.0163	-0.0051	-0.0059	0.0257	-0.0012	0.0067
*Agoseris glauca**	Compositae	1	0.0196	0.0051	0.0044	-0.0094	-0.0056	-0.0150	-0.0138	-0.0032	-0.0098	0.0094
*Agoseris retrorsa**	Compositae	1	0.0537	-0.0144	-0.0290	-0.0073	0.0010	-0.0033	0.0053	0.0870	-0.0098	0.0390
Agropyron cristatum€	Gramineae	1	0.0689	-0.0204	-0.0142	-0.0112	-0.0099	-0.0150	0.0458	0.0565	-0.0012	-0.0085
Agrostis exarata	Gramineae	3	-0.0189	-0.0164	-0.0469	-0.0211	0.0083	-0.0207	-0.0332	0.0416	0.1570	0.3453
*Agrostis scabra**	Gramineae	1	-0.0109	-0.0204	-0.0291	-0.0027	0.0370	0.0140	-0.0138	0.0581	0.2611	0.1104
Agrostis stolonifera€	Gramineae	2	-0.0109	-0.0183	-0.0329	-0.0240	-0.0163	-0.0248	-0.0217	0.0068	0.0093	0.2268
*Allium acuminatum**	Liliaceae	9	-0.0113	-0.0403	-0.0317	0.0492	-0.0213	-0.0161	0.0051	0.0793	-0.0269	0.0119
Allium macropetalum‡*	Liliaceae	1	-0.0109	-0.0156	-0.0064	0.0599	0.1228	-0.0033	-0.0045	-0.0055	-0.0098	-0.0085
*Allium nevadense**	Liliaceae	1	-0.0109	-0.0204	-0.0216	0.0856	-0.0029	-0.0024	-0.0019	-0.0127	-0.0098	-0.0085
Allium sp.	Liliaceae	2	0.0062	-0.0075	-0.0014	0.0303	0.1292	-0.0282	-0.0252	-0.0061	0.0107	0.0006
Amelanchier alnifolia	Rosaceae	11	-0.0245	-0.0668	-0.0809	-0.0447	0.0231	0.0570	0.0507	0.2711	0.1498	0.0627

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Amelanchier utahensis	Rosaceae	141	-0.0900	-0.0968	0.1661	0.0340	-0.0081	0.1990	0.1598	-0.0446	-0.0817	-0.1249
Andropogon gerardii	Gramineae	3	0.0543	-0.0164	-0.0358	-0.0027	0.0669	-0.0177	-0.0232	-0.0220	0.0281	0.1007
*Androstephium breviflorum**	Liliaceae	18	0.1286	0.0230	0.0268	0.0390	-0.0266	-0.0414	0.0075	-0.0162	-0.0299	-0.0159
*Angelica pinnata**	Umbelliferae	1	-0.0109	-0.0204	-0.0291	-0.0027	0.0370	0.0140	-0.0138	0.0581	0.2611	0.1104
*Antennaria microphylla**	Compositae	1	-0.0109	-0.0159	-0.0063	0.0034	-0.0035	-0.0150	-0.0138	-0.0127	-0.0098	-0.0085
*Antennaria parvifolia**	Compositae	2	-0.0154	0.0083	0.0049	0.0489	0.0019	-0.0122	-0.0054	-0.0136	-0.0139	-0.0121
Antennaria rosulata‡*	Compositae	3	-0.0189	-0.0276	-0.0021	-0.0057	0.0238	0.0195	0.0148	0.0635	0.1447	0.0540
Apocynum androsaemifolium	Apocynaceae	2	-0.0154	-0.0290	-0.0414	-0.0189	0.0270	0.0152	-0.0030	0.0476	0.2110	0.0817
*Aquilegia chrysantha**	Ranunculaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	0.0179	-0.0085
*Aquilegia formosa**	Ranunculaceae	3	-0.0189	-0.0355	-0.0509	-0.0269	0.0919	-0.0250	-0.0232	-0.0163	0.0585	-0.0070
Aquilegia sp.	Ranunculaceae	2	-0.0154	-0.0290	-0.0466	-0.0286	0.0010	-0.0147	-0.0238	0.0385	0.1668	-0.0025
Arabis hirsuta‡*	Cruciferae	1	-0.0109	-0.0204	0.0010	-0.0035	-0.0109	0.0065	0.0428	0.0474	-0.0098	-0.0085
Arabis perennans	Cruciferae	124	-0.0953	0.0295	0.2379	0.0173	0.0178	0.0472	0.0240	-0.0499	-0.0301	-0.0931
*Aralia racemosa**	Araliaceae	3	-0.0189	-0.0331	-0.0507	-0.0417	-0.0017	-0.0187	-0.0151	0.0313	0.2012	0.0469
Arceuthobium abietinum‡*	Viscaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0054	-0.0132	-0.0124	0.0096	0.0963	0.0050
*Arceuthobium divaricatum**	Viscaceae	5	-0.0245	-0.0183	0.1003	0.0123	-0.0047	0.0106	0.0083	-0.0202	-0.0220	-0.0192
*Arceuthobium vaginatum**	Viscaceae	1	-0.0109	-0.0204	-0.0368	-0.0097	-0.0109	0.0411	0.0110	0.0214	-0.0016	-0.0085
Arctostaphylos patula	Ericaceae	94	-0.1013	-0.0593	0.1132	0.2147	0.0767	0.0893	0.0301	-0.0959	-0.0837	-0.0949
Arenaria fendleri	Caryophyllaceae	23	-0.0544	-0.0513	-0.0408	0.1880	0.2407	-0.0605	-0.0522	-0.0512	-0.0203	-0.0427
Arenaria macradenia	Caryophyllaceae	46	-0.0804	-0.0607	0.1271	0.0990	0.1502	-0.0052	-0.0069	-0.0401	-0.0037	-0.0588
*Arenaria pusilla**	Caryophyllaceae	1	-0.0109	0.0189	-0.0059	0.0579	0.0148	-0.0132	-0.0124	-0.0127	-0.0098	-0.0085
*Argemone munita**	Papaveraceae	1	0.0512	-0.0001	-0.0138	-0.0240	-0.0163	-0.0150	-0.0138	-0.0058	-0.0098	-0.0085
*Aristida purpurea**	Gramineae	26	0.0216	0.1291	0.0011	-0.0051	-0.0026	-0.0986	-0.0888	-0.0646	-0.0393	0.0031
*Arnica cordifolia**	Compositae	1	-0.0109	-0.0204	-0.0142	-0.0097	-0.0041	0.0778	0.0034	-0.0004	-0.0098	-0.0085
Artemisia arbuscula[1]	Compositae	4	0.0383	-0.0411	-0.0399	-0.0278	-0.0146	0.0007	0.0998	0.1245	0.0005	-0.0095
Artemisia campestris	Compositae	14	-0.0334	-0.0471	-0.0323	0.2341	-0.0044	-0.0462	-0.0361	-0.0341	-0.0315	-0.0327
Artemisia dracunculus	Compositae	12	0.0695	-0.0227	-0.0022	-0.0069	-0.0291	-0.0208	-0.0178	-0.0225	-0.0260	-0.0138
Artemisia filifolia	Compositae	3	-0.0189	0.0497	-0.0347	-0.0349	-0.0250	-0.0431	-0.0308	-0.0220	-0.0170	-0.0016
*Artemisia frigida**	Compositae	1	-0.0109	-0.0204	-0.0216	-0.0115	0.0069	0.0247	0.0354	0.0580	-0.0016	-0.0085
Artemisia ludoviciana	Compositae	51	-0.0089	0.0007	0.1161	0.0261	0.0346	-0.0376	-0.0201	0.0195	0.0962	0.1026
Artemisia sp.	Compositae	2	-0.0154	-0.0198	-0.0370	-0.0290	-0.0196	-0.0352	-0.0308	0.0197	0.0312	0.4632

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Artemisia tridentata	Compositae	55	0.0211	0.0237	0.0140	0.0087	-0.0941	-0.0650	-0.0307	-0.0021	-0.0710	-0.0200
Asclepias subverticillata	Asclepiadaceae	9	0.0355	0.0465	-0.0005	-0.0368	-0.0372	0.0539	-0.0149	-0.0385	-0.0264	-0.0193
Aster glaucodes	Compositae	6	-0.0269	-0.0144	0.0115	-0.0389	-0.0091	-0.0054	-0.0173	0.0135	0.1160	0.1156
Aster sp.	Compositae	1	0.0207	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	-0.0016	0.0906
*Aster spathulatus**‡‡	Compositae	1	0.0290	-0.0204	-0.0220	-0.0177	-0.0099	0.0355	0.0251	0.0679	0.0050	-0.0085
*Aster welshii**	Compositae	6	-0.0269	-0.0449	-0.0609	-0.0507	-0.0144	-0.0372	-0.0375	0.0224	0.1633	0.1134
Astragalus flavus	Leguminosae	1	-0.0109	0.0218	-0.0287	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Astragalus lancearius**	Leguminosae	1	-0.0109	-0.0084	0.0175	0.0125	0.0009	-0.0051	-0.0059	0.0109	-0.0043	-0.0085
*Astragalus mollissimus**	Leguminosae	1	-0.0109	0.0220	-0.0290	-0.0240	-0.0163	-0.0248	-0.0098	-0.0127	-0.0098	0.0144
*Astragalus nuttallianus**	Leguminosae	9	0.0317	0.2167	-0.0609	-0.0709	-0.0475	-0.0755	-0.0594	-0.0385	-0.0297	-0.0260
*Astragalus piutensis**	Leguminosae	6	0.0388	-0.0222	-0.0177	-0.0238	-0.0305	0.0101	0.0300	0.0813	-0.0118	0.0003
Astragalus sp.	Leguminosae	27	-0.0026	0.0839	0.0152	0.0117	-0.0543	-0.0184	0.0463	-0.0225	-0.0394	0.0038
Astragalus subcinereus	Leguminosae	1	-0.0109	-0.0161	0.0011	-0.0175	-0.0163	0.0356	0.0140	-0.0065	-0.0098	-0.0085
*Astragalus zionis**	Leguminosae	22	-0.0192	-0.0059	0.0676	0.0727	0.0065	0.0252	0.0815	0.0117	-0.0376	-0.0311
Atriplex canescens	Chenopodiaceae	10	0.2722	0.0716	-0.0649	-0.0708	-0.0447	-0.0797	-0.0634	-0.0407	-0.0314	-0.0275
Atriplex confertifolia	Chenopodiaceae	2	0.0099	0.0251	-0.0303	-0.0295	-0.0231	-0.0352	-0.0308	-0.0179	-0.0139	-0.0121
Baccharis salicina	Compositae	3	-0.0189	-0.0139	-0.0469	-0.0335	-0.0226	-0.0431	-0.0377	0.0088	0.0332	0.4594
Baileya multiradiata	Compositae	8	0.0310	0.2654	-0.0188	-0.0432	-0.0368	-0.0711	-0.0622	-0.0363	-0.0280	-0.0245
Balsamorhiza sagittata	Compositae	8	-0.0169	-0.0466	0.0013	-0.0108	-0.0278	0.1063	0.2200	0.0523	-0.0256	-0.0245
*Berula erecta**	Umbelliferae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
*Betula occidentalis**	Betulaceae	2	-0.0154	-0.0224	-0.0114	-0.0192	0.0012	-0.0007	-0.0086	0.0070	0.0529	0.0360
*Bouteloua curtipendula**	Gramineae	2	-0.0154	-0.0189	-0.0342	-0.0030	0.0629	-0.0352	-0.0308	-0.0179	-0.0089	-0.0121
*Bouteloua eriopoda**	Gramineae	5	0.0220	0.2274	-0.0295	-0.0540	-0.0316	-0.0514	-0.0453	-0.0285	-0.0220	-0.0192
Bouteloua gracilis	Gramineae	19	-0.0244	-0.0350	-0.0107	0.1887	-0.0281	-0.0236	0.0192	-0.0029	-0.0361	-0.0306
Brickellia californica	Compositae	4	-0.0066	0.0351	0.0451	-0.0051	0.0036	-0.0400	-0.0357	-0.0125	-0.0159	-0.0082
Brickellia grandiflora	Compositae	10	-0.0350	-0.0516	-0.0105	0.0153	0.1977	0.0232	-0.0173	0.0078	0.1723	0.0031
Brickellia microphylla	Compositae	5	-0.0245	0.0370	0.0673	-0.0131	0.0217	-0.0240	-0.0234	-0.0285	-0.0092	-0.0192
*Brickellia oblongifolia**‡‡	Compositae	2	-0.0154	-0.0055	-0.0153	-0.0251	0.0119	-0.0192	-0.0252	0.0050	0.0747	-0.0025
Bromus anomalus	Gramineae	5	0.0436	-0.0421	-0.0621	-0.0175	-0.0099	-0.0147	0.0014	0.1586	0.1089	0.0533
*Bromus carinatus**	Gramineae	9	-0.0196	-0.0434	-0.0574	-0.0456	-0.0372	-0.0416	-0.0107	0.2714	0.0118	0.2511
*Bromus ciliatus**	Gramineae	12	0.0293	-0.0670	-0.0665	-0.0486	0.0757	-0.0176	-0.0460	0.0473	0.2602	0.0995

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Bromus diandrus€	Gramineae	10	0.0312	-0.0336	-0.0857	-0.0613	-0.0407	-0.0734	-0.0647	-0.0126	0.0071	0.3353
Bromus rubens€	Gramineae	43	0.0339	0.3680	0.0731	-0.0990	-0.0855	-0.1439	-0.1239	-0.0865	-0.0642	-0.0544
Bromus tectorum€	Gramineae	130	0.1156	0.2135	0.0710	-0.0590	-0.1214	-0.1832	-0.1512	-0.1083	-0.0873	0.0262
Bromus vulgaris‡*	Gramineae	1	0.0606	-0.0162	-0.0368	-0.0149	-0.0099	-0.0033	0.0053	0.0953	-0.0016	-0.0085
Calamagrostis scopulorum	Gramineae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	0.0179	-0.0085
*Calochortus flexuosus**	Liliaceae	7	0.0171	0.1303	-0.0365	-0.0562	-0.0395	-0.0626	-0.0550	-0.0302	-0.0261	-0.0160
Calochortus nuttallii	Liliaceae	23	0.0711	0.0121	0.0399	0.0553	-0.0340	-0.0119	-0.0077	0.0074	-0.0329	-0.0153
*Camissonia multijuga**	Onagraceae	1	-0.0109	0.0127	0.0000	-0.0240	-0.0100	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Camissonia parvula**	Onagraceae	2	-0.0154	0.0040	0.0322	0.0436	-0.0006	0.0107	0.0060	-0.0112	-0.0100	-0.0121
Camissonia sp.*	Onagraceae	1	-0.0109	-0.0117	-0.0232	-0.0169	-0.0113	-0.0248	-0.0217	0.0263	0.0371	0.3576
Cardamine cordifolia‡‡*	Cruciferae	1	0.0606	-0.0204	-0.0368	-0.0169	0.0454	-0.0248	-0.0217	-0.0127	0.0547	0.0050
*Carex aurea**	Cyperaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0099	0.0014	-0.0138	0.0403	0.0491	0.0067
*Carex hystericina**	Cyperaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	0.0179	-0.0085
Carex occidentalis	Cyperaceae	1	-0.0109	-0.0204	-0.0213	0.0098	0.0029	-0.0248	-0.0217	0.0176	0.0465	0.0870
Carex rossii	Cyperaceae	67	-0.0335	-0.1431	-0.0482	0.0505	0.1222	0.2114	0.1553	0.1027	0.0042	-0.0554
Carex sp.	Cyperaceae	7	-0.0291	-0.0347	-0.0301	0.0315	0.0308	-0.0238	-0.0291	-0.0045	0.0800	0.0708
Castilleja chromosa	Scrophulariaceae	2	-0.0154	-0.0260	-0.0198	0.0174	-0.0022	-0.0212	-0.0196	0.0086	0.0260	0.0556
Castilleja linariifolia	Scrophulariaceae	7	0.0512	-0.0182	-0.0071	-0.0227	-0.0003	0.0218	0.1229	0.0230	0.0120	-0.0101
*Castilleja scabrida**	Scrophulariaceae	40	-0.0392	-0.0544	-0.0185	0.0831	0.2903	-0.0401	-0.0609	-0.0449	0.0430	-0.0458
Caulanthus cooperi‡*	Cruciferae	1	0.1112	-0.0117	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Caulanthus crassicaulis**	Cruciferae	1	-0.0109	-0.0154	-0.0030	-0.0240	-0.0163	0.0103	0.0039	0.0036	-0.0098	-0.0085
Ceanothus martinii	Rhamnaceae	4	0.0182	-0.0389	0.0003	-0.0180	-0.0174	0.1121	0.0788	0.0641	-0.0055	-0.0172
Celtis reticulata	Ulmaceae	2	0.0233	-0.0197	-0.0411	-0.0143	-0.0196	-0.0282	-0.0252	-0.0179	-0.0139	0.0235
Cenchrus longispinus	Gramineae	2	0.0017	-0.0198	-0.0425	-0.0290	-0.0196	-0.0352	-0.0308	0.0097	0.0264	0.2903
*Centaurium exaltatum**	Gentianaceae	1	0.0196	0.0051	0.0044	-0.0094	-0.0056	-0.0150	-0.0138	-0.0032	-0.0098	0.0094
*Centrostegia thurberi**	Polygonaceae	3	-0.0189	0.1220	-0.0116	-0.0303	-0.0221	-0.0431	-0.0263	-0.0220	-0.0170	-0.0149
Cercocarpus intricatus	Rosaceae	40	-0.0741	-0.0732	-0.0008	0.0948	0.3022	-0.0254	-0.0425	-0.0540	0.0241	-0.0535
Cercocarpus montanus	Rosaceae	33	-0.0411	-0.0845	0.0125	-0.0766	-0.0614	0.2588	0.1440	-0.0299	-0.0468	-0.0521
Chaenactis douglasii	Compositae	44	-0.0625	-0.0719	0.1114	0.2527	0.1140	-0.0008	0.0032	-0.0622	-0.0409	-0.0586
Chaenactis stevioides	Compositae	1	-0.0109	0.0466	-0.0212	-0.0177	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Chaetopappa ericoides	Compositae	1	-0.0109	-0.0115	0.0011	-0.0177	-0.0163	0.1087	0.0330	-0.0065	-0.0098	-0.0085

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Chamaesyce albomarginata	Euphorbiaceae	23	0.2085	0.0081	-0.0514	-0.0601	-0.0683	0.0486	0.0045	-0.0518	-0.0427	-0.0065
Chamaesyce fendleri	Euphorbiaceae	3	-0.0189	0.0881	0.0804	0.0042	-0.0212	-0.0075	-0.0240	-0.0220	-0.0170	-0.0149
Chenopodium fremontii	Chenopodiaceae	3	-0.0189	-0.0138	-0.0414	-0.0259	-0.0284	-0.0203	0.0029	0.1983	-0.0100	0.0605
*Chimaphila menziesii**	Pyrolaceae	5	-0.0245	-0.0460	-0.0491	-0.0310	0.0634	0.0085	-0.0139	0.0322	0.1943	0.0404
Chimaphila umbellata‡	Pyrolaceae	1	-0.0109	-0.0204	-0.0291	-0.0027	0.0370	0.0140	-0.0138	0.0581	0.2611	0.1104
Chorispora tenella€*	Cruciferae	1	0.1195	0.0037	-0.0215	-0.0240	-0.0163	-0.0150	-0.0138	-0.0127	0.0002	0.0114
*Chrysopsis jonesii**	Compositae	1	-0.0109	-0.0204	-0.0290	-0.0054	0.0507	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Chrysopsis villosa	Compositae	74	-0.0433	-0.0529	0.0206	0.1933	0.1966	-0.0952	-0.0770	-0.0592	0.0364	0.0487
Chrysothamnus depressus	Compositae	5	0.0294	-0.0360	-0.0271	-0.0197	-0.0127	0.0345	0.1618	0.0621	-0.0145	-0.0192
Chrysothamnus greenei‡*	Compositae	1	-0.0109	0.0045	0.0285	-0.0112	-0.0104	-0.0023	-0.0037	-0.0127	-0.0098	-0.0085
Chrysothamnus nauseosus	Compositae	39	-0.0081	0.0136	0.0303	0.1202	-0.0282	-0.0941	-0.0726	-0.0711	-0.0435	0.0411
Chrysothamnus parryi	Compositae	1	-0.0109	-0.0204	-0.0142	0.0130	-0.0109	0.0987	0.0279	-0.0032	-0.0098	-0.0085
Chrysothamnus viscidiflorus	Compositae	6	0.0518	0.0138	0.0050	0.0321	-0.0334	0.0095	0.0182	0.0337	-0.0206	-0.0211
Cirsium arizonicum	Compositae	16	0.0236	-0.0538	0.0075	0.0434	0.1052	0.0028	-0.0078	0.0262	0.0954	0.0911
Cirsium wheeleri	Compositae	8	0.2224	-0.0308	-0.0508	-0.0337	-0.0135	0.0147	0.0741	0.0514	0.0035	-0.0196
Clematis columbiana	Ranunculaceae	3	-0.0006	-0.0355	-0.0552	-0.0252	0.0046	0.0343	-0.0085	0.0509	0.0859	0.0117
Coleogyne ramosissima	Rosaceae	13	0.0145	0.2448	-0.0393	-0.0830	-0.0601	-0.0914	-0.0800	-0.0466	-0.0360	-0.0315
Collinsia parviflora	Scrophulariaceae	2	-0.0154	-0.0255	-0.0199	0.0254	0.0755	-0.0060	-0.0005	0.0123	-0.0139	-0.0121
*Collomia grandiflora**	Polemoniaceae	4	-0.0219	-0.0178	0.0063	0.0087	0.0116	0.0250	0.0349	0.0067	0.0337	-0.0095
Collomia linearis‡‡*	Polemoniaceae	2	0.0286	0.0019	-0.0082	-0.0276	-0.0231	-0.0142	-0.0006	0.0544	-0.0139	0.0120
Comandra umbellata	Santalaceae	35	-0.0686	-0.0696	0.0777	0.1314	0.0282	0.0257	0.0821	-0.0146	-0.0470	-0.0505
Convolvulus arvensis€	Convolvulaceae	1	-0.0109	0.0235	-0.0212	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Cordylanthus kingii	Scrophulariaceae	19	-0.0072	0.0745	0.0772	-0.0369	-0.0655	0.0145	0.0030	-0.0393	-0.0440	-0.0342
Cordylanthus sp.	Scrophulariaceae	1	-0.0109	0.0330	0.0669	-0.0240	-0.0163	-0.0150	-0.0138	-0.0127	-0.0098	-0.0085
*Cornus sericea**	Cornaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0054	-0.0132	-0.0124	0.0096	0.0963	0.0050
Crepis acuminata‡‡*	Compositae	3	-0.0189	-0.0118	0.0150	0.0580	0.0018	-0.0193	-0.0003	-0.0178	-0.0170	-0.0149
*Crepis occidentalis**	Compositae	1	-0.0109	0.0151	0.0314	-0.0097	-0.0104	0.0103	-0.0059	-0.0127	-0.0098	-0.0085
Crepis runcinata‡*	Compositae	2	-0.0154	-0.0156	-0.0085	0.0443	-0.0092	-0.0212	-0.0112	-0.0129	-0.0139	-0.0121
Crepis sp.	Compositae	2	0.0411	-0.0224	-0.0006	-0.0101	-0.0065	-0.0166	0.0171	0.0406	0.0260	0.0264
*Cryptantha cinerea**	Boraginaceae	17	-0.0462	-0.0177	0.0358	0.2622	-0.0157	-0.0466	-0.0341	-0.0226	-0.0398	-0.0325
Cryptantha circumscissa‡‡*	Boraginaceae	3	0.0018	0.0247	-0.0137	0.0253	-0.0223	-0.0301	-0.0204	-0.0178	-0.0170	-0.0149

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
*Cryptantha confertiflora**	Boraginaceae	31	-0.0351	0.0704	0.1252	0.0887	0.0972	-0.0691	-0.0637	-0.0683	-0.0403	-0.0469
*Cryptantha fendleri**	Boraginaceae	2	0.0286	-0.0031	-0.0284	-0.0251	-0.0231	-0.0282	-0.0252	-0.0131	-0.0139	-0.0121
Cryptantha humilis	Boraginaceae	1	-0.0109	-0.0111	-0.0095	-0.0240	-0.0163	-0.0248	-0.0028	-0.0127	-0.0098	-0.0085
Cryptantha sp. (annual)	Boraginaceae	60	-0.0026	0.2085	0.1317	0.0211	-0.0596	-0.1192	-0.0796	-0.0746	-0.0776	-0.0639
*Cucurbita foetidissima**	Cucurbitaceae	1	0.1155	-0.0117	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Cymopterus newberryi**	Umbelliferae	1	-0.0109	-0.0106	0.0414	0.1042	-0.0083	-0.0248	-0.0119	0.0007	-0.0098	-0.0085
*Cymopterus purpureus**	Umbelliferae	15	-0.0240	0.0333	0.0497	-0.0356	-0.0408	0.1293	0.0713	-0.0351	-0.0388	-0.0339
Cymopterus sp.*	Umbelliferae	1	0.0133	0.0499	-0.0212	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Cystopteris fragilis**	Polypodiaceae	6	0.0155	-0.0505	-0.0547	-0.0311	0.0833	-0.0160	-0.0366	0.0764	0.3184	0.0691
Dactylis glomerata€	Gramineae	2	-0.0154	-0.0239	-0.0466	-0.0211	-0.0231	-0.0129	0.0009	0.3368	-0.0020	0.0686
Dalea searlsiae	Leguminosae	13	0.0076	0.1213	0.0237	-0.0688	-0.0565	-0.0649	-0.0570	-0.0412	-0.0360	-0.0315
Datura wrightii	Solanaceae	3	-0.0049	-0.0306	-0.0595	-0.0417	-0.0284	-0.0374	-0.0332	-0.0138	-0.0073	0.2023
*Delphinium andersonii**	Ranunculaceae	1	-0.0109	-0.0106	0.0414	0.1042	-0.0083	-0.0248	-0.0119	0.0007	-0.0098	-0.0085
*Delphinium nuttallianum**	Ranunculaceae	7	-0.0061	-0.0339	-0.0169	-0.0119	-0.0293	0.0741	0.0510	0.0040	-0.0172	-0.0141
*Descurainia californica**	Cruciferae	1	0.0779	-0.0084	-0.0142	-0.0007	-0.0045	0.0076	0.0500	0.0264	-0.0098	-0.0085
Descurainia pinnata	Cruciferae	28	-0.0037	0.1716	0.0713	-0.0494	-0.0819	-0.0556	-0.0588	0.0116	-0.0520	-0.0214
Descurainia sophia€*	Cruciferae	1	-0.0109	-0.0204	-0.0279	-0.0165	-0.0163	-0.0150	0.0115	0.0787	-0.0016	0.0103
*Disporum trachycarpum**	Liliaceae	4	-0.0219	-0.0411	-0.0482	-0.0337	0.0665	0.0404	-0.0081	0.0632	0.2342	0.0494
Distichlis spicata	Gramineae	1	-0.0109	0.0039	-0.0287	-0.0169	-0.0113	-0.0248	-0.0217	-0.0127	0.0131	0.1908
*Dodecatheon pulchellum**	Primulaceae	2	-0.0154	-0.0290	-0.0469	-0.0340	-0.0108	-0.0123	-0.0086	-0.0025	0.0387	-0.0025
*Draba asprella**	Cruciferae	33	-0.0516	-0.0823	0.0124	0.0971	0.2068	0.0802	0.0067	-0.0115	0.1409	-0.0142
*Draba cuneifolia**	Cruciferae	1	0.0196	0.0051	0.0044	-0.0094	-0.0056	-0.0150	-0.0138	-0.0032	-0.0098	0.0094
Draba verna‡‡‡€*	Cruciferae	40	0.0217	0.2595	0.0867	-0.0141	-0.0704	-0.0816	-0.0745	-0.0737	-0.0615	-0.0189
Dracocephalum parviflorum	Labiatae	1	0.0207	-0.0110	-0.0216	0.0050	-0.0113	0.0014	-0.0040	0.0148	-0.0098	-0.0085
*Dryopteris filix-mas**	Polypodiaceae	2	-0.0154	-0.0290	-0.0467	-0.0189	0.0224	0.0006	-0.0186	0.0479	0.2531	0.0817
Echinocereus engelmannii	Cactaceae	7	0.0099	0.0998	0.0162	-0.0347	-0.0267	-0.0588	-0.0520	-0.0302	-0.0261	-0.0229
Echinocereus triglochidiatus	Cactaceae	22	-0.0407	0.1003	0.1300	0.0608	0.0065	-0.0478	-0.0232	-0.0488	-0.0394	-0.0377
*Eleocharis palustris**	Cyperaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
*Eleocharis parishii**	Cyperaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
Elymus canadensis	Gramineae	4	-0.0219	-0.0346	-0.0516	-0.0170	0.0062	-0.0254	-0.0357	0.0581	0.2267	0.2742
Elymus elymoides	Gramineae	58	0.0162	0.0923	0.0099	0.0133	0.0141	-0.0536	-0.0274	-0.0206	-0.0247	-0.0314

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Elymus hispidus€	Gramineae	1	-0.0109	-0.0116	0.0146	-0.0026	-0.0053	-0.0051	-0.0059	-0.0127	-0.0043	-0.0085
Elymus smithii‡‡‡[2]	Gramineae	3	0.1929	-0.0112	-0.0420	-0.0185	-0.0115	-0.0119	0.0309	0.0583	-0.0170	0.0127
Elymus sp.	Gramineae	2	-0.0109	-0.0139	-0.0177	-0.0046	-0.0111	-0.0100	-0.0099	-0.0091	-0.0098	-0.0085
Elymus spicatus	Gramineae	6	0.0722	-0.0048	-0.0195	-0.0271	-0.0193	0.0027	0.0116	0.0236	-0.0167	-0.0055
*Elymus trachycaulus**	Gramineae	10	-0.0042	-0.0334	-0.0334	-0.0351	-0.0399	-0.0503	-0.0244	0.1829	0.0698	0.2409
*Encelia frutescens**	Compositae	4	0.0475	0.1980	-0.0583	-0.0451	-0.0328	-0.0499	-0.0436	-0.0255	-0.0197	-0.0172
Ephedra nevadensis	Ephedraceae	18	0.0478	0.2637	0.0091	-0.0872	-0.0630	-0.0888	-0.0854	-0.0554	-0.0394	-0.0374
Ephedra viridis	Ephedraceae	16	-0.0215	0.0204	0.0730	0.0153	-0.0456	-0.0459	-0.0326	-0.0466	-0.0366	-0.0303
Epilobium brachycarpum	Onagraceae	3	-0.0189	-0.0331	-0.0461	0.0110	-0.0058	-0.0317	-0.0286	0.0187	0.1830	0.0390
*Epilobium ciliatum**	Onagraceae	3	0.0225	-0.0355	-0.0595	-0.0253	0.0420	-0.0055	-0.0286	0.0497	0.1889	0.0707
Epilobium glandulosum‡*	Onagraceae	3	-0.0006	-0.0355	-0.0417	-0.0060	0.0404	0.0018	-0.0286	0.0690	0.2225	0.1360
Epilobium sp.	Onagraceae	1	-0.0109	-0.0204	-0.0279	-0.0165	-0.0163	-0.0150	0.0115	0.0787	-0.0016	0.0103
*Epipactis gigantea**	Orchidaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	0.0179	-0.0085
Equisetum arvense	Equisetaceae	1	-0.0109	-0.0117	-0.0232	-0.0169	-0.0113	-0.0248	-0.0217	0.0263	0.0371	0.3576
Equisetum hyemale	Equisetaceae	8	0.0242	-0.0422	-0.0812	-0.0464	-0.0190	-0.0501	-0.0537	0.0372	0.1603	0.3744
Equisetum laevigatum	Equisetaceae	2	-0.0154	-0.0260	-0.0466	-0.0340	-0.0231	-0.0352	-0.0308	0.0097	0.0132	0.3213
*Eriastrum eremicum**	Polemoniaceae	7	-0.0062	0.2058	0.0095	-0.0395	-0.0417	-0.0626	-0.0550	-0.0339	-0.0261	-0.0229
*Eriastrum sparsiflorum**	Polemoniaceae	13	0.0561	0.1752	-0.0212	-0.0568	-0.0495	-0.0914	-0.0710	-0.0466	-0.0360	-0.0250
*Erigeron canaani**	Compositae	16	-0.0448	-0.0719	-0.0209	0.1198	0.2338	0.0168	-0.0131	-0.0192	0.0259	-0.0316
Erigeron divergens	Compositae	17	-0.0097	-0.0041	0.0203	-0.0308	-0.0587	-0.0115	0.0173	0.0552	-0.0393	-0.0170
*Erigeron flagellaris**	Compositae	2	-0.0154	-0.0198	-0.0127	-0.0103	0.0322	-0.0077	-0.0252	0.0184	0.0885	0.2472
Erigeron pumilus	Compositae	1	-0.0109	-0.0116	0.0146	-0.0026	-0.0053	-0.0051	-0.0059	-0.0127	-0.0043	-0.0085
*Erigeron religious**	Compositae	1	-0.0109	-0.0001	-0.0138	0.0062	0.0029	0.0233	0.0284	0.0007	-0.0098	-0.0085
*Erigeron sionis**	Compositae	4	-0.0219	-0.0387	-0.0358	0.0211	0.2217	0.0074	-0.0145	0.0187	0.1662	0.0426
Erigeron sp.	Compositae	14	0.0183	-0.0196	0.0122	0.0569	-0.0271	0.0253	0.0560	-0.0216	-0.0246	0.0674
Erigeron speciosus	Compositae	6	0.0224	-0.0409	-0.0374	-0.0328	-0.0154	0.0479	0.0804	0.1538	0.0046	0.0143
Erigeron utahensis	Compositae	41	-0.0341	0.1342	0.2246	0.0464	-0.0274	-0.0700	-0.0681	-0.0713	-0.0588	-0.0560
*Eriogonum alatum**	Polygonaceae	6	-0.0269	-0.0291	-0.0297	0.2047	0.0216	-0.0118	-0.0125	-0.0224	-0.0147	-0.0211
Eriogonum corymbosum	Polygonaceae	4	0.0057	0.0237	-0.0251	-0.0224	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Eriogonum davidsonii**	Polygonaceae	32	-0.0379	0.1334	0.1227	0.0399	-0.0310	-0.0761	-0.0554	-0.0592	-0.0503	-0.0478
Eriogonum fasciculatum	Polygonaceae	3	-0.0189	0.0211	0.0748	-0.0180	-0.0206	0.0043	-0.0128	-0.0220	-0.0170	-0.0149

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*Eriogonum heracleoides**‡	Polygonaceae	1	-0.0109	-0.0204	-0.0216	0.0856	-0.0029	-0.0024	-0.0019	-0.0127	-0.0098	-0.0085
Eriogonum inflatum	Polygonaceae	3	0.0610	0.1657	-0.0459	-0.0381	-0.0284	-0.0431	-0.0377	-0.0220	-0.0170	-0.0149
*Eriogonum jamesii**	Polygonaceae	10	-0.0350	-0.0338	-0.0469	0.0466	0.2322	-0.0553	-0.0502	-0.0361	-0.0065	-0.0275
Eriogonum microthecum	Polygonaceae	15	0.0519	0.0652	0.0645	-0.0408	-0.0378	-0.0589	-0.0519	-0.0245	-0.0305	-0.0290
*Eriogonum palmerianum**	Polygonaceae	15	0.0092	0.2175	0.0316	-0.0719	-0.0476	-0.0797	-0.0779	-0.0503	-0.0369	-0.0339
Eriogonum racemosum	Polygonaceae	59	-0.0291	-0.0898	0.0990	0.1001	0.0704	-0.0038	0.0302	0.0394	0.0517	-0.0253
Eriogonum sp.	Polygonaceae	7	-0.0291	0.0333	0.0162	-0.0002	-0.0297	-0.0475	-0.0430	-0.0339	-0.0261	-0.0229
Eriogonum umbellatum	Polygonaceae	21	-0.0382	-0.0305	0.0243	0.1447	0.0862	-0.0200	0.0085	-0.0145	0.0074	-0.0264
*Erioneuron pilosum**‡	Gramineae	2	0.0099	0.1098	-0.0356	-0.0208	0.0332	-0.0352	-0.0308	-0.0179	-0.0139	-0.0121
Erodium cicutarium€	Geraniaceae	10	0.2865	0.1277	-0.0910	-0.0748	-0.0488	-0.0766	-0.0609	-0.0407	-0.0282	-0.0211
Erysimum asperum	Cruciferae	64	-0.0775	-0.0340	0.2064	0.1601	-0.0076	0.0100	0.0369	-0.0315	-0.0287	-0.0527
*Eupatorium herbaceum**	Compositae	12	-0.0081	-0.0709	-0.0670	-0.0391	0.1492	0.0054	-0.0365	0.0630	0.3612	0.0462
Euphorbia brachycera	Euphorbiaceae	5	0.0414	-0.0382	-0.0518	0.0127	-0.0217	0.0515	0.0060	-0.0243	-0.0220	-0.0192
*Euphorbia spathulata**	Euphorbiaceae	1	0.3561	0.0035	-0.0293	-0.0240	-0.0163	-0.0248	-0.0020	-0.0127	-0.0098	-0.0085
Fendlerella utahensis	Saxifragaceae	1	-0.0109	-0.0204	0.0064	-0.0240	0.0168	0.0473	0.0135	-0.0127	-0.0030	-0.0085
Festuca octoflora	Gramineae	74	0.0169	0.2480	0.0657	0.0993	-0.0069	-0.1467	-0.1123	-0.0946	-0.0819	-0.0469
Fraxinus anomala	Oleaceae	45	-0.0588	0.0431	0.2408	-0.0204	0.0183	0.0824	0.0020	-0.0571	-0.0092	-0.0520
Fraxinus velutina	Oleaceae	6	-0.0169	-0.0349	-0.0638	-0.0478	-0.0313	-0.0546	-0.0496	-0.0130	0.0263	0.1862
*Fritillaria atropurpurea**	Liliaceae	9	-0.0225	-0.0276	0.0404	0.1442	-0.0179	-0.0199	0.0025	-0.0235	-0.0153	-0.0260
*Gaillardia pinnatifida**	Compositae	2	0.0770	0.0830	-0.0413	-0.0340	-0.0231	-0.0282	-0.0252	-0.0179	-0.0068	0.0020
Galium aparine	Rubiaceae	6	-0.0144	-0.0180	-0.0198	-0.0275	-0.0202	-0.0195	-0.0191	0.0417	0.0227	0.0290
*Galium bifolium**	Rubiaceae	2	0.0411	-0.0290	-0.0306	-0.0185	-0.0185	-0.0130	0.0362	0.2181	0.0041	0.0247
*Galium multiflorum**	Rubiaceae	28	-0.0557	-0.0715	0.1091	0.0320	0.0953	0.0121	-0.0059	-0.0183	0.0520	-0.0249
Galium sp.	Rubiaceae	1	0.0196	0.0007	0.0788	-0.0020	-0.0163	0.0014	-0.0040	-0.0065	-0.0098	-0.0085
*Galium trifidum**	Rubiaceae	2	-0.0154	-0.0194	0.0132	-0.0006	0.0406	0.0039	-0.0252	0.0003	0.0890	0.0264
*Galium triflorum**	Rubiaceae	4	-0.0219	-0.0174	-0.0340	-0.0375	0.0169	-0.0196	-0.0310	0.0434	0.2616	0.0562
*Garrya flavescens**	Garryaceae	9	-0.0331	-0.0363	0.0376	-0.0030	-0.0256	0.0300	-0.0135	-0.0232	-0.0226	-0.0260
*Gaura coccinea**	Onagraceae	1	0.0249	0.1296	-0.0287	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Gayophytum sp.	Onagraceae	14	0.0125	-0.0316	-0.0370	-0.0369	-0.0406	0.0238	0.0777	0.1380	-0.0272	0.0207
*Geranium richardsonii**‡‡	Geraniaceae	1	-0.0109	-0.0204	-0.0291	-0.0027	0.0370	0.0140	-0.0138	0.0581	0.2611	0.1104
*Gilia inconspicua**	Polemoniaceae	84	-0.0137	0.2558	0.1513	0.0515	-0.1029	-0.1116	-0.0963	-0.1140	-0.0969	-0.0584

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*Gilia scopulorum**‡‡‡	Polemoniaceae	1	-0.0109	0.0004	0.0031	0.0269	-0.0163	0.0112	-0.0059	0.0014	-0.0098	-0.0085
*Glycyrrhiza lepidota**	Leguminosae	1	0.1195	0.0037	-0.0215	-0.0240	-0.0163	-0.0150	-0.0138	-0.0127	0.0002	0.0114
*Gnaphalium wrightii**	Compositae	9	-0.0331	-0.0003	0.0182	0.0485	0.0870	-0.0346	-0.0305	0.0031	0.1052	0.0465
*Goodyera oblongifolia**	Orchidaceae	5	-0.0245	-0.0460	-0.0690	-0.0374	0.0260	0.0369	-0.0076	0.0882	0.2131	0.0404
Grindelia squarrosa	Compositae	1	0.0449	-0.0117	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Gutierrezia sp.[3]	Compositae	94	0.0989	0.2817	0.0670	-0.0696	-0.0984	-0.1590	-0.1114	-0.1043	-0.0962	-0.0086
*Hackelia patens**	Boraginaceae	5	0.0219	-0.0146	0.0180	0.0033	-0.0109	-0.0110	-0.0057	0.0411	-0.0125	-0.0192
*Haplopappus armerioides**‡	Compositae	1	-0.0109	-0.0204	-0.0294	-0.0174	-0.0163	0.1376	0.0257	-0.0127	-0.0098	-0.0085
Haplopappus gracilis	Compositae	4	0.1243	-0.0202	-0.0699	-0.0411	-0.0278	-0.0449	-0.0397	-0.0255	-0.0081	0.1083
Haplopappus laricifolius‡	Compositae	1	0.0207	0.0772	0.0151	-0.0240	-0.0106	-0.0150	-0.0138	-0.0127	-0.0098	-0.0085
Haplopappus scopulorum	Compositae	42	-0.0620	-0.0438	0.1804	0.0711	0.0046	0.0255	0.0324	-0.0509	-0.0055	-0.0515
*Helianthella quinquenervis**	Compositae	1	-0.0109	-0.0161	-0.0052	-0.0165	-0.0099	0.0461	0.1300	-0.0058	-0.0098	-0.0085
*Helianthus annuus**	Compositae	2	0.0241	-0.0166	-0.0522	-0.0340	-0.0231	-0.0352	-0.0308	-0.0179	-0.0139	0.0057
*Helianthus anomalus**‡‡	Compositae	2	0.3310	-0.0058	-0.0468	-0.0340	-0.0231	-0.0352	-0.0168	-0.0179	-0.0139	-0.0121
*Helianthus nuttallii**‡‡	Compositae	2	-0.0154	-0.0290	-0.0069	-0.0193	-0.0185	0.0860	0.1539	-0.0021	-0.0139	-0.0121
Heuchera rubescens	Saxifragaceae	12	-0.0292	-0.0709	-0.0461	-0.0292	0.1744	0.0382	-0.0019	0.0476	0.2533	-0.0007
*Hieracium fendleri**‡‡	Compositae	1	-0.0109	-0.0156	-0.0138	0.0744	0.0327	0.0093	-0.0045	-0.0055	0.0131	-0.0085
Hilaria sp.	Gramineae	41	0.1280	0.2507	0.0402	-0.1195	-0.0871	-0.1262	-0.1138	-0.0683	-0.0675	-0.0510
Holodiscus dumosus	Rosaceae	21	-0.0356	-0.0921	-0.0438	0.0077	0.3078	-0.0046	-0.0308	-0.0027	0.1947	-0.0222
*Hordeum murinum**€	Gramineae	1	0.3561	0.0035	-0.0293	-0.0240	-0.0163	-0.0248	-0.0020	-0.0127	-0.0098	-0.0085
Hordeum sp.	Gramineae	1	-0.0109	0.0044	-0.0049	0.0480	0.0072	-0.0248	-0.0119	-0.0065	-0.0098	-0.0085
Hydrophyllum occidentale	Hydrophyllaceae	2	-0.0154	-0.0290	-0.0359	-0.0251	0.0522	0.0165	-0.0130	0.0432	0.1573	-0.0025
Hymenopappus filifolius	Compositae	11	-0.0368	-0.0381	-0.0048	0.2352	-0.0077	-0.0134	-0.0248	-0.0122	-0.0309	-0.0242
*Hymenoxys cooperi**	Compositae	5	0.1070	0.0776	0.0185	-0.0390	-0.0263	-0.0291	-0.0196	0.0033	-0.0183	-0.0192
Ipomopsis aggregata	Polemoniaceae	5	-0.0027	0.0176	0.0435	0.0043	-0.0292	0.0541	0.1344	-0.0049	-0.0220	-0.0112
Ipomopsis congesta	Polemoniaceae	14	-0.0417	-0.0395	0.0396	0.1277	0.0315	-0.0169	-0.0247	-0.0114	-0.0070	-0.0024
*Iva axillaris**	Compositae	1	-0.0109	-0.0117	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	0.0166
Ivesia sabulosa	Rosaceae	7	-0.0291	-0.0435	-0.0373	0.0594	0.2693	-0.0287	-0.0318	-0.0284	0.0105	-0.0229
*Jamesia americana**	Saxifragaceae	2	0.0352	-0.0260	-0.0466	-0.0290	0.0206	-0.0282	-0.0252	0.0007	0.1444	0.0538
Juncus arcticus	Juncaceae	3	-0.0189	-0.0305	-0.0471	-0.0180	-0.0143	-0.0431	-0.0377	0.0325	0.0552	0.3103
Juncus ensifolius	Juncaceae	2	-0.0154	-0.0228	-0.0425	-0.0290	-0.0150	-0.0166	-0.0252	0.0472	0.0611	0.2580

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Juncus tenuis	Juncaceae	1	-0.0109	-0.0117	-0.0232	-0.0169	-0.0113	-0.0248	-0.0217	0.0263	0.0371	0.3576
Juniperus osteosperma	Cupressaceae	115	0.0251	0.1706	0.1868	-0.0462	-0.1486	0.0226	0.0318	-0.1258	-0.1273	-0.1076
Juniperus scopulorum	Cupressaceae	21	-0.0178	-0.0775	-0.0461	-0.0170	-0.0283	0.0539	0.0409	0.1754	0.0134	0.0109
Koeleria macrantha	Gramineae	1	0.0689	-0.0159	-0.0217	0.0052	-0.0109	0.0235	0.0359	0.0344	-0.0098	-0.0085
Lactuca serriola€	Compositae	13	0.2237	-0.0045	-0.0836	-0.0662	-0.0233	-0.0521	-0.0387	0.0166	0.0243	0.0185
*Lactuca tatarica**	Compositae	2	0.0069	-0.0223	-0.0359	0.0017	0.0182	0.0109	-0.0126	0.0516	0.1780	0.0721
*Lappula occidentalis**	Boraginaceae	2	0.0352	-0.0143	-0.0326	-0.0223	-0.0116	-0.0129	0.0009	0.0628	-0.0028	-0.0121
Lathyrus brachycalyx	Leguminosae	9	-0.0331	-0.0063	0.0917	-0.0259	-0.0346	0.0058	-0.0064	-0.0323	-0.0297	-0.0260
*Lathyrus lanszwertii**	Leguminosae	20	-0.0150	-0.0783	-0.0283	-0.0158	-0.0433	0.1446	0.2432	0.0463	-0.0253	-0.0321
*Layia glandulosa**	Compositae	2	-0.0154	0.0319	0.0088	0.0161	-0.0090	-0.0122	-0.0124	-0.0112	-0.0100	-0.0121
Lepidium campestre‡‡€*	Cruciferae	1	-0.0109	-0.0204	-0.0294	-0.0240	-0.0163	-0.0033	0.0053	0.1108	0.0136	0.0067
*Lepidium densiflorum**	Cruciferae	8	0.1484	0.1408	-0.0475	-0.0499	-0.0344	-0.0559	-0.0466	-0.0341	-0.0254	-0.0245
*Lepidium fremontii**	Cruciferae	1	0.0196	0.0550	-0.0107	-0.0177	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Lepidium lasiocarpum**	Cruciferae	1	0.1195	0.0037	-0.0215	-0.0240	-0.0163	-0.0150	-0.0138	-0.0127	0.0002	0.0114
*Lepidium montanum**	Cruciferae	1	0.0537	-0.0144	-0.0290	-0.0073	0.0010	-0.0033	0.0053	0.0870	-0.0098	0.0390
Leptodactylon pungens	Polemoniaceae	8	-0.0312	-0.0489	-0.0113	0.0261	0.2160	0.0105	0.0036	-0.0213	0.0551	-0.0196
Leptodactylon watsonii	Polemoniaceae	10	-0.0350	0.0074	0.0209	0.0080	0.0732	-0.0228	-0.0311	-0.0149	0.0196	-0.0275
Leucocrinum montanum‡*	Liliaceae	1	-0.0109	0.0073	0.0119	0.0210	-0.0045	0.0076	0.0042	-0.0127	-0.0098	-0.0085
Linanthastrum nuttallii	Polemoniaceae	19	-0.0433	-0.0681	0.0315	0.1760	0.1762	-0.0110	-0.0309	-0.0092	0.0617	-0.0090
*Linanthus dichotomus**	Polemoniaceae	14	0.0000	0.1643	0.0400	-0.0073	-0.0175	-0.0784	-0.0666	-0.0485	-0.0335	-0.0265
Linum perenne€	Linaceae	6	-0.0070	-0.0198	0.0699	0.0251	0.0469	0.0372	0.0333	-0.0255	0.0071	-0.0134
*Lithophragma tenellum**	Saxifragaceae	1	-0.0109	-0.0071	-0.0067	-0.0149	-0.0163	-0.0051	-0.0059	0.0257	-0.0012	0.0067
*Lithospermum incisum**	Boraginaceae	2	0.0017	0.0099	0.0067	-0.0246	-0.0231	0.0576	0.0026	-0.0131	-0.0139	-0.0121
*Lithospermum ruderale**	Boraginaceae	2	0.0524	-0.0114	-0.0033	0.0115	-0.0150	-0.0027	0.0386	0.0680	-0.0080	0.0006
*Lomatium dissectum**	Umbelliferae	4	-0.0219	-0.0389	-0.0354	-0.0296	-0.0269	-0.0035	0.0358	0.1080	-0.0067	0.0000
Lomatium graveolens	Umbelliferae	1	-0.0109	-0.0204	-0.0290	-0.0240	0.0469	0.0256	-0.0045	0.0413	0.1068	-0.0085
Lomatium sp.	Umbelliferae	1	-0.0109	-0.0159	-0.0063	0.0034	-0.0035	-0.0150	-0.0138	-0.0127	-0.0098	-0.0085
*Lotus denticulatus**	Leguminosae	6	0.1489	0.0262	-0.0177	-0.0513	-0.0379	-0.0439	-0.0235	-0.0285	-0.0242	-0.0211
*Lotus plebeius**	Leguminosae	17	-0.0171	0.1402	0.1080	0.0393	-0.0188	-0.0600	-0.0524	-0.0514	-0.0374	-0.0363
*Lotus utahensis**	Leguminosae	12	0.0040	-0.0308	-0.0165	-0.0260	-0.0268	0.0389	0.1321	0.0350	-0.0305	-0.0162
Lupinus argenteus	Leguminosae	1	-0.0109	0.0903	0.0057	-0.0106	-0.0056	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
*Lupinus brevicaulis**	Leguminosae	4	-0.0219	0.0659	-0.0162	-0.0376	-0.0303	-0.0449	-0.0298	-0.0255	-0.0197	-0.0172
Lupinus concinnus	Leguminosae	1	-0.0109	0.0722	0.0141	0.0133	-0.0056	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Lupinus kingii**	Leguminosae	2	-0.0154	0.0136	-0.0176	-0.0142	-0.0231	-0.0002	0.0474	-0.0036	-0.0139	-0.0121
Lupinus sericeus	Leguminosae	9	0.0692	-0.0536	-0.0838	-0.0294	-0.0299	0.0016	0.0436	0.2937	-0.0064	0.0352
*Lychnis drummondii**	Caryophyllaceae	1	-0.0109	-0.0114	-0.0124	0.0988	0.0029	-0.0248	-0.0217	0.0355	-0.0098	0.0067
Lycium pallidum	Solanaceae	3	0.3355	0.0067	-0.0506	-0.0376	-0.0255	-0.0431	-0.0263	-0.0220	-0.0170	-0.0149
Lygodesmia grandiflora	Compositae	2	-0.0154	0.0277	0.0124	0.0441	-0.0193	-0.0122	-0.0040	-0.0129	-0.0139	-0.0121
Machaeranthera canescens	Compositae	40	-0.0036	0.0284	0.0883	0.1432	-0.0142	-0.0414	-0.0210	-0.0066	-0.0534	-0.0318
Mahonia repens	Berberidaceae	29	-0.0231	-0.0947	-0.0511	-0.0508	-0.0046	0.1614	0.0969	0.0752	0.1310	0.0000
Medicago lupulina€	Leguminosae	1	-0.0109	-0.0162	-0.0290	-0.0240	-0.0163	-0.0248	-0.0217	0.0015	0.0070	0.2964
Melilotus alba€*	Leguminosae	2	0.0993	-0.0119	-0.0413	-0.0340	-0.0231	-0.0282	-0.0252	-0.0003	-0.0010	0.0723
Melilotus officinalis€	Leguminosae	1	-0.0109	0.0039	-0.0287	-0.0169	-0.0113	-0.0248	-0.0217	-0.0127	0.0131	0.1908
Melilotus sp. €	Leguminosae	2	-0.0154	-0.0198	-0.0370	-0.0290	-0.0196	-0.0352	-0.0308	0.0197	0.0312	0.4632
*Mentzelia integra**	Loasaceae	1	0.0554	0.0417	-0.0293	-0.0177	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Mertensia arizonica	Boraginaceae	7	-0.0044	-0.0469	-0.0832	-0.0364	-0.0166	-0.0108	0.0021	0.2907	0.0961	0.1045
*Mertensia fusiformis**	Boraginaceae	3	-0.0189	-0.0260	-0.0181	-0.0255	-0.0106	0.1384	0.1672	-0.0149	-0.0170	-0.0149
*Microseris lindleyi**	Compositae	8	0.0141	0.0280	0.0754	0.0552	-0.0134	-0.0329	-0.0171	-0.0204	-0.0223	-0.0211
*Microsteris gracilis**	Polemoniaceae	28	-0.0384	-0.0110	0.0462	0.0624	0.0171	-0.0096	0.0168	0.0556	-0.0135	-0.0144
*Mimulus cardinalis**	Scrophulariaceae	2	-0.0154	-0.0260	-0.0466	-0.0340	-0.0231	-0.0282	-0.0252	0.0007	0.1183	0.0442
*Mimulus floribundus**	Scrophulariaceae	1	-0.0109	0.0337	0.0295	0.0488	0.0036	-0.0150	-0.0138	-0.0127	-0.0098	-0.0085
*Mimulus guttatus**	Scrophulariaceae	3	-0.0189	-0.0331	-0.0550	-0.0294	0.0063	0.0002	-0.0240	0.0649	0.2451	0.1089
*Mimulus parryi**	Scrophulariaceae	1	-0.0109	0.0073	0.0119	0.0210	-0.0045	0.0076	0.0042	-0.0127	-0.0098	-0.0085
Mirabilis multiflora	Nyctaginaceae	7	0.1470	0.1333	-0.0178	-0.0565	-0.0365	-0.0588	-0.0442	-0.0339	-0.0223	-0.0152
Mirabilis pumila‡‡*	Nyctaginaceae	1	0.0491	0.0152	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Monardella odoratissima	Labiatae	6	0.0025	-0.0488	-0.0627	-0.0131	0.1961	-0.0348	-0.0324	-0.0244	0.0404	-0.0155
Montia perfoliata	Portulacaceae	3	-0.0189	-0.0110	0.0469	0.0374	0.0018	-0.0149	-0.0227	-0.0033	0.0138	0.0167
Muhlenbergia asperifolia	Gramineae	2	0.0770	-0.0089	-0.0358	-0.0340	-0.0231	-0.0282	-0.0252	-0.0079	0.0051	0.2180
Muhlenbergia montana	Gramineae	2	-0.0154	-0.0224	-0.0306	0.0769	0.0860	-0.0117	-0.0120	-0.0129	-0.0045	-0.0121
*Muhlenbergia pungens**	Gramineae	5	-0.0245	-0.0001	-0.0069	0.1187	-0.0227	-0.0316	-0.0295	-0.0253	-0.0220	-0.0192
Muhlenbergia racemosa	Gramineae	3	-0.0006	-0.0355	-0.0507	-0.0256	0.0293	0.0018	-0.0286	0.0515	0.2055	0.0806
Muhlenbergia sp.	Gramineae	1	-0.0109	-0.0115	0.0011	-0.0177	-0.0163	0.1087	0.0330	-0.0065	-0.0098	-0.0085

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Muhlenbergia thurberi	Gramineae	12	-0.0174	-0.0610	-0.0526	0.0809	0.2838	-0.0207	-0.0274	-0.0274	0.0811	-0.0182
*Myosurus cupulatus**	Ranunculaceae	1	-0.0109	-0.0068	0.0019	-0.0177	-0.0163	0.0014	-0.0138	-0.0127	-0.0098	-0.0085
Nasturtium officinale	Cruciferae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
*Navarretia breweri**	Polemoniaceae	5	0.0225	-0.0303	-0.0351	-0.0051	-0.0103	0.0073	0.0645	0.0414	-0.0220	0.0022
Nicotiana attenuata	Solanaceae	1	0.0512	-0.0001	-0.0138	-0.0240	-0.0163	-0.0150	-0.0138	-0.0058	-0.0098	-0.0085
Oenothera caespitosa	Onagraceae	9	-0.0033	-0.0030	0.0777	0.0068	-0.0066	0.0235	0.0220	-0.0001	-0.0194	-0.0139
Oenothera longissima	Onagraceae	2	-0.0154	-0.0198	-0.0370	-0.0290	-0.0196	-0.0352	-0.0308	0.0197	0.0312	0.4632
Oenothera pallida	Onagraceae	12	-0.0224	0.0081	0.0494	0.1056	-0.0116	-0.0433	-0.0436	-0.0284	-0.0092	0.1363
Oenothera sp.	Onagraceae	2	0.1635	-0.0057	-0.0413	-0.0340	-0.0231	-0.0282	-0.0252	-0.0179	-0.0068	0.0020
Opuntia erinacea	Cactaceae	17	-0.0068	0.2280	0.0095	-0.0750	-0.0492	-0.0720	-0.0542	-0.0497	-0.0380	-0.0261
Opuntia macrorhiza	Cactaceae	120	-0.0871	0.0051	0.1969	0.2100	0.0551	0.0113	0.0278	-0.0893	-0.0880	-0.1079
Opuntia phaeacantha	Cactaceae	9	0.1030	0.0449	0.0187	0.0060	-0.0339	-0.0589	-0.0420	-0.0291	-0.0297	-0.0200
Opuntia polyacantha‡‡	Cactaceae	3	-0.0189	0.0721	-0.0325	-0.0381	-0.0284	-0.0431	-0.0377	-0.0220	-0.0170	-0.0149
Opuntia whipplei	Cactaceae	3	0.0158	0.0719	-0.0459	-0.0339	-0.0255	-0.0431	-0.0377	-0.0220	-0.0170	-0.0149
*Orobanche fasciculata**	Orobanchaceae	2	-0.0154	-0.0220	0.0088	0.1714	0.0019	-0.0282	-0.0098	-0.0085	-0.0139	-0.0121
Orobanche uniflora‡‡*	Orobanchaceae	1	-0.0109	-0.0026	0.0039	0.0039	-0.0163	0.0246	0.0886	0.0076	-0.0098	-0.0085
*Oryzopsis micrantha**	Gramineae	2	-0.0154	-0.0254	0.0236	-0.0089	-0.0003	0.0515	-0.0018	0.0008	-0.0089	0.0012
Osmorhiza occidentalis	Umbelliferae	4	-0.0060	-0.0258	-0.0429	-0.0358	0.0221	0.0098	-0.0047	0.1617	0.1010	0.0541
Pachystima myrsinites	Celastraceae	54	-0.0573	-0.1407	-0.0118	0.0118	0.0706	0.2096	0.1310	0.0248	0.1121	-0.0386
Panicum sp.*	Gramineae	2	-0.0154	-0.0052	-0.0199	0.0220	-0.0029	-0.0352	-0.0238	0.0140	0.0194	0.2472
*Pectocarya setosa**	Boraginaceae	3	0.0226	0.0666	-0.0321	-0.0339	-0.0255	-0.0431	-0.0263	-0.0220	-0.0170	-0.0149
*Pedicularis centranthera**	Scrophulariaceae	10	-0.0194	-0.0305	0.0315	-0.0249	-0.0408	0.1849	0.1029	-0.0235	-0.0314	-0.0275
*Pediomelum mephiticum**	Leguminosae	2	0.0069	0.0005	0.0142	-0.0157	-0.0231	0.0063	0.0156	-0.0179	-0.0139	-0.0121
*Pellaea truncata**	Polypodiaceae	1	-0.0109	-0.0008	0.0154	-0.0174	-0.0163	-0.0033	-0.0045	-0.0058	-0.0098	-0.0085
Penstemon angustifolius‡*	Scrophulariaceae	38	-0.0262	-0.0539	0.0177	0.0474	0.0685	0.0513	0.0048	0.0071	0.0290	-0.0272
*Penstemon barbatus**	Scrophulariaceae	6	-0.0269	-0.0216	0.0152	0.0110	0.0565	0.0150	0.0015	0.0004	0.1087	0.0279
Penstemon comarrhenus	Scrophulariaceae	2	0.0017	0.0004	0.0249	0.0411	-0.0196	0.0076	0.0306	0.0016	-0.0139	0.0006
*Penstemon confusus**	Scrophulariaceae	3	-0.0189	-0.0032	0.0457	-0.0067	-0.0143	-0.0244	-0.0117	-0.0220	-0.0170	-0.0149
Penstemon eatonii	Scrophulariaceae	23	-0.0439	0.0296	0.1760	0.0390	-0.0203	-0.0281	-0.0238	-0.0371	-0.0302	0.0407
Penstemon higginsii	Scrophulariaceae	5	-0.0245	-0.0318	-0.0169	-0.0317	-0.0180	0.0574	0.0720	0.0924	-0.0099	-0.0124
Penstemon humilis	Scrophulariaceae	27	-0.0593	-0.0565	0.0790	0.1052	0.2021	-0.0007	-0.0125	-0.0374	0.0411	-0.0438

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
*Penstemon laevis**	Scrophulariaceae	26	-0.0532	-0.0162	0.0773	0.2316	0.0846	-0.0416	-0.0335	-0.0542	-0.0342	-0.0456
Penstemon linarioides	Scrophulariaceae	13	0.0007	-0.0437	-0.0164	-0.0284	-0.0471	0.0904	0.2105	0.0331	-0.0360	-0.0167
Penstemon pachyphyllus	Scrophulariaceae	1	-0.0109	0.0759	0.0043	-0.0034	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Penstemon palmeri	Scrophulariaceae	19	-0.0032	0.1018	0.0837	-0.0440	-0.0310	-0.0624	-0.0480	-0.0468	-0.0295	0.0380
Penstemon rostriflorus	Scrophulariaceae	30	-0.0179	-0.0415	0.0496	-0.0137	0.1297	0.0101	-0.0091	0.0460	0.1111	-0.0184
Peraphyllum ramosissimum	Rosaceae	10	-0.0016	-0.0473	-0.0258	-0.0263	-0.0351	0.1847	0.2389	0.0165	-0.0293	-0.0275
*Perityle tenella**	Compositae	1	-0.0109	-0.0204	-0.0368	-0.0240	0.0041	-0.0248	-0.0217	-0.0127	0.0277	0.0050
*Peteria thompsoniae**	Leguminosae	5	0.0215	0.1095	-0.0140	-0.0511	-0.0311	-0.0559	-0.0489	-0.0254	-0.0220	-0.0192
Petradoria pumila	Compositae	2	0.0128	-0.0290	-0.0066	0.0259	0.0074	-0.0060	0.0762	0.0069	-0.0139	-0.0121
Petrophytum caespitosum	Rosaceae	12	-0.0385	-0.0612	-0.0582	0.0268	0.3143	0.0020	-0.0243	-0.0130	0.1274	0.0088
*Phacelia fremontii**	Hydrophyllaceae	6	-0.0144	0.1215	0.0457	-0.0356	-0.0354	-0.0399	-0.0365	-0.0313	-0.0242	-0.0211
Phacelia heterophylla	Hydrophyllaceae	42	-0.0498	-0.0651	0.0028	0.0973	0.0148	-0.0231	-0.0256	0.1026	0.0676	0.1188
*Phacelia ivesiana**	Hydrophyllaceae	1	0.0196	0.0051	0.0044	-0.0094	-0.0056	-0.0150	-0.0138	-0.0032	-0.0098	0.0094
*Phacelia palmeri**	Hydrophyllaceae	1	0.0554	0.0417	-0.0293	-0.0177	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
*Philadelphus microphyllus**	Saxifragaceae	10	-0.0248	-0.0600	-0.0154	-0.0246	0.1294	0.0352	-0.0116	0.0565	0.2350	0.0047
Phlox austromontana	Polemoniaceae	54	-0.0767	-0.0520	0.1251	0.1886	0.0721	0.0491	0.0433	-0.0512	-0.0503	-0.0675
*Phlox longifolia**	Polemoniaceae	11	0.0053	-0.0238	0.0293	-0.0061	-0.0282	0.1193	0.2187	-0.0028	-0.0293	-0.0234
Phoradendron juniperinum	Viscaceae	14	-0.0331	-0.0010	0.1106	0.0545	-0.0285	0.0484	0.0399	-0.0264	-0.0335	-0.0327
Phragmites australis	Gramineae	2	-0.0154	-0.0087	-0.0409	-0.0290	-0.0196	-0.0352	-0.0308	-0.0079	0.0143	0.3451
Physalis hederifolia	Solanaceae	8	0.0857	-0.0088	-0.0355	-0.0285	-0.0332	0.0003	-0.0346	-0.0226	-0.0044	0.0376
*Physalis longifolia**	Solanaceae	1	0.1195	0.0037	-0.0215	-0.0240	-0.0163	-0.0150	-0.0138	-0.0127	0.0002	0.0114
Physaria chambersii	Cruciferae	3	-0.0049	-0.0200	0.0859	-0.0097	-0.0166	0.0871	0.0155	-0.0220	-0.0170	-0.0149
*Physaria ludoviciana**	Cruciferae	3	-0.0189	0.0209	0.0691	0.1120	-0.0154	-0.0187	-0.0113	-0.0137	-0.0170	-0.0149
Physaria newberryi	Cruciferae	7	-0.0106	-0.0018	0.0068	-0.0185	-0.0416	0.1630	0.0418	-0.0279	-0.0261	-0.0229
*Physaria rectipes**	Cruciferae	3	-0.0189	-0.0058	0.0326	0.1040	-0.0168	-0.0187	-0.0125	-0.0143	-0.0170	-0.0149
*Physaria wardii**	Cruciferae	1	-0.0109	-0.0161	-0.0141	-0.0163	0.0010	0.0474	0.2013	-0.0065	-0.0098	-0.0085
*Physocarpus alternans**	Rosaceae	1	-0.0109	-0.0204	0.0064	-0.0240	0.0168	0.0473	0.0135	-0.0127	-0.0030	-0.0085
Pinus edulis	Pinaceae	53	-0.0363	-0.0799	0.0969	0.0150	-0.0519	0.2160	0.1513	-0.0540	-0.0481	-0.0640
Pinus monophylla	Pinaceae	64	-0.0639	0.1617	0.1964	-0.0616	-0.1071	-0.1054	-0.0930	-0.0808	-0.0790	-0.0597
Pinus ponderosa	Pinaceae	60	-0.0574	-0.1236	-0.0675	0.1735	0.1993	0.0611	0.0717	-0.0050	0.0285	-0.0322
Plantago patagonica	Plantaginaceae	13	0.1238	0.1362	-0.0524	0.0399	-0.0229	-0.0564	-0.0376	-0.0292	-0.0360	-0.0315

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
*Poa bigelovii**	Gramineae	8	0.0487	0.1065	-0.0240	-0.0542	-0.0388	-0.0675	-0.0593	-0.0329	-0.0280	-0.0181
Poa bulbosa€*	Gramineae	1	0.0848	-0.0162	-0.0368	-0.0169	-0.0113	-0.0248	-0.0217	-0.0127	-0.0016	0.0094
Poa compressa€*	Gramineae	3	0.0185	-0.0296	-0.0550	-0.0320	-0.0183	-0.0307	-0.0221	0.0583	0.0051	0.2434
Poa fendleriana	Gramineae	190	-0.1391	-0.0620	0.2132	0.1283	0.1186	0.0577	0.0891	-0.0417	-0.0072	-0.0837
Poa pratensis€	Gramineae	14	-0.0045	-0.0598	-0.0991	-0.0276	-0.0409	-0.0455	-0.0258	0.2466	0.0391	0.2027
Poa secunda	Gramineae	4	-0.0219	-0.0150	0.0621	0.0318	0.0205	-0.0237	-0.0227	-0.0207	-0.0162	-0.0172
Poa sp.	Gramineae	1	0.0196	0.0257	0.0239	-0.0177	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Polygonum douglasii	Polygonaceae	39	-0.0015	-0.0693	-0.0321	0.1548	0.0311	0.0050	0.0855	0.1711	-0.0403	-0.0010
Polypodium hesperium	Polypodiaceae	6	-0.0269	-0.0470	-0.0363	-0.0402	0.0592	-0.0031	-0.0263	0.0408	0.2726	0.0228
Populus fremontii	Salicaceae	6	-0.0139	-0.0177	-0.0756	-0.0534	-0.0362	-0.0613	-0.0487	0.0008	0.0149	0.3936
Populus tremuloides	Salicaceae	2	-0.0154	-0.0290	-0.0359	-0.0100	-0.0095	-0.0199	-0.0116	0.0909	0.0426	0.0664
Prunus virginiana	Rosaceae	10	0.0293	-0.0582	-0.0766	-0.0404	-0.0332	0.0307	0.0676	0.2923	0.0006	0.0201
Pseudotsuga menziesii	Pinaceae	18	-0.0476	-0.0849	-0.0415	-0.0183	0.1328	0.0553	0.0042	0.0309	0.2559	0.0212
*Psoralidium lanceolatum**	Leguminosae	4	0.0437	0.0173	-0.0447	-0.0232	-0.0303	-0.0449	-0.0337	-0.0255	-0.0146	0.0044
Psorothamnus fremontii	Leguminosae	11	0.0240	0.2031	-0.0107	-0.0679	-0.0532	-0.0747	-0.0660	-0.0428	-0.0330	-0.0289
Pteridium aquilinum	Polypodiaceae	3	-0.0189	-0.0327	-0.0371	0.0472	0.0421	-0.0009	-0.0232	0.0407	0.1626	0.1094
Pterospora andromedea	Monotropaceae	2	-0.0154	-0.0204	-0.0137	-0.0027	-0.0071	-0.0007	-0.0126	0.0241	0.0224	-0.0121
Purshia mexicana	Rosaceae	15	-0.0140	0.0794	0.0437	-0.0691	-0.0602	-0.0049	-0.0317	-0.0468	-0.0388	-0.0339
Purshia tridentata	Rosaceae	36	-0.0398	-0.0642	0.0241	0.0959	-0.0355	0.1318	0.1832	-0.0297	-0.0563	-0.0475
Quercus gambelii	Fagaceae	135	-0.0835	-0.2123	-0.0259	0.0354	0.0422	0.1792	0.1804	0.1418	0.0666	-0.0480
Quercus turbinella	Fagaceae	50	-0.0617	0.1136	0.2131	0.0456	-0.0280	-0.0980	-0.0825	-0.0805	-0.0597	-0.0524
*Ranunculus andersonii**	Ranunculaceae	1	-0.0109	0.0337	0.0295	0.0488	0.0036	-0.0150	-0.0138	-0.0127	-0.0098	-0.0085
Ranunculus sp.*	Ranunculaceae	1	-0.0109	-0.0117	-0.0232	-0.0169	-0.0113	-0.0248	-0.0217	0.0263	0.0371	0.3576
Ranunculus testiculatus€*	Ranunculaceae	2	0.0241	-0.0166	-0.0522	-0.0340	-0.0231	-0.0352	-0.0308	-0.0179	-0.0139	0.0057
Rhus aromatica	Anacardiaceae	23	-0.0011	0.1709	0.1113	-0.0483	-0.0489	-0.0629	-0.0392	-0.0439	-0.0425	-0.0388
*Ribes velutinum**	Saxifragaceae	1	-0.0109	-0.0161	0.0011	-0.0175	-0.0079	-0.0051	-0.0059	-0.0058	-0.0035	-0.0085
*Robinia neomexicana**	Leguminosae	1	-0.0109	0.0029	0.0022	-0.0149	-0.0163	-0.0051	0.0130	0.0826	-0.0098	0.0255
Rosa woodsii	Rosaceae	12	0.0277	-0.0648	-0.0878	-0.0490	-0.0177	0.0722	0.0501	0.2403	0.0501	0.0438
Rubia tinctoria€*	Rubiaceae	1	0.1195	0.0037	-0.0215	-0.0240	-0.0163	-0.0150	-0.0138	-0.0127	0.0002	0.0114
*Rubus leucodermis**	Rosaceae	4	-0.0219	-0.0390	-0.0585	-0.0420	0.0088	-0.0278	-0.0310	0.0373	0.2611	0.0432
Rumex hymenosepalus	Polygonaceae	2	0.0912	0.0270	-0.0411	-0.0340	-0.0231	-0.0352	-0.0308	-0.0179	-0.0139	-0.0121

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Salix exigua	Salicaceae	3	-0.0189	-0.0139	-0.0469	-0.0335	-0.0226	-0.0431	-0.0377	0.0088	0.0332	0.4594
Salix scouleriana	Salicaceae	2	-0.0154	-0.0290	-0.0466	-0.0340	-0.0185	-0.0166	-0.0182	0.0239	0.0423	0.0246
Salvia dorrii	Labiatae	3	-0.0189	0.0757	0.0290	-0.0148	-0.0249	-0.0301	-0.0273	-0.0220	-0.0170	-0.0149
*Samolus floribundus**	Primulaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
*Saxifraga rhomboidea**	Saxifragaceae	1	-0.0109	-0.0159	-0.0006	0.0311	0.0898	0.0053	-0.0092	-0.0029	0.0390	-0.0085
*Scirpus microcarpus**	Cyperaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
*Scirpus pungens**	Cyperaceae	1	-0.0109	0.0039	-0.0287	-0.0169	-0.0113	-0.0248	-0.0217	-0.0127	0.0131	0.1908
Secale cereale€*	Gramineae	2	-0.0154	-0.0197	-0.0464	-0.0340	-0.0231	-0.0282	-0.0252	-0.0179	-0.0139	-0.0121
*Sedum debile**	Crassulaceae	2	-0.0154	-0.0290	-0.0064	-0.0009	0.1569	-0.0060	-0.0005	0.0304	0.0922	-0.0025
*Sedum lanceolatum**	Crassulaceae	3	-0.0189	-0.0245	-0.0156	0.1417	0.1751	-0.0182	-0.0178	-0.0095	0.0031	-0.0149
*Selaginella underwoodii**	Selaginellaceae	17	-0.0462	-0.0703	-0.0063	0.0248	0.2741	0.0094	-0.0260	0.0099	0.1728	-0.0180
*Selaginella utahensis**	Selaginellaceae	2	-0.0154	-0.0255	-0.0142	0.0623	0.1932	-0.0269	-0.0242	-0.0129	0.0264	-0.0121
Selaginella watsonii‡‡*	Selaginellaceae	1	-0.0109	-0.0015	0.0336	0.0405	0.0036	0.0076	0.0042	-0.0032	-0.0043	-0.0085
Senecio eremophilus	Compositae	3	-0.0189	-0.0314	-0.0552	-0.0312	-0.0284	-0.0125	0.0038	0.3109	0.0063	0.0600
Senecio hydrophilus‡*	Compositae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
Senecio multilobatus	Compositae	99	-0.0802	-0.1087	0.1615	0.1919	0.1136	0.0662	0.0478	-0.0288	-0.0054	-0.0606
Senecio spartioides	Compositae	26	-0.0242	-0.0684	-0.0308	0.0456	0.0257	-0.0538	-0.0629	0.0085	0.1054	0.0200
*Shepherdia rotundifolia**	Elaeagnaceae	17	-0.0160	0.1196	0.1785	-0.0524	-0.0565	-0.0523	-0.0547	-0.0453	-0.0397	-0.0271
*Silene antirrhina**	Caryophyllaceae	3	-0.0189	0.0432	0.0061	0.0642	0.0129	-0.0307	-0.0278	-0.0178	-0.0131	0.0034
*Silene verecunda**	Caryophyllaceae	5	-0.0245	-0.0317	0.0558	0.0450	0.0094	0.0048	-0.0040	-0.0124	-0.0171	-0.0192
Sisymbrium altissimum€	Cruciferae	4	0.0640	0.0076	-0.0258	-0.0328	-0.0249	-0.0350	-0.0222	0.0272	-0.0197	0.0090
Sisymbrium irio‡‡€*	Cruciferae	2	0.0271	0.0024	-0.0425	-0.0290	-0.0196	-0.0352	-0.0308	0.0097	0.0194	0.2472
Smilacina racemosa	Liliaceae	6	-0.0139	-0.0488	-0.0248	-0.0427	0.0917	0.0248	-0.0148	0.0463	0.2531	0.0089
Smilacina stellata	Liliaceae	3	-0.0189	-0.0355	-0.0640	-0.0334	-0.0215	0.0102	-0.0142	0.0284	0.0379	-0.0060
Solanum sarrachoides€*	Solanaceae	1	-0.0109	-0.0162	-0.0368	-0.0123	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Solanum sp.	Solanaceae	1	-0.0109	-0.0162	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Solidago velutina	Compositae	38	0.0085	-0.1190	-0.0889	0.0046	0.1890	0.0614	0.1036	0.0889	0.1476	-0.0134
Sonchus sp.* €	Compositae	3	-0.0006	-0.0280	-0.0428	-0.0338	0.0013	-0.0207	-0.0332	0.0413	0.0915	0.3652
Sphaeralcea ambigua	Malvaceae	2	-0.0154	-0.0100	-0.0176	-0.0142	-0.0231	0.0068	0.0530	-0.0036	-0.0139	-0.0121
Sphaeralcea grossulariifolia	Malvaceae	14	0.2053	0.0710	-0.0075	-0.0691	-0.0565	-0.0771	-0.0643	-0.0423	-0.0347	-0.0224
*Sphaeralcea parvifolia**	Malvaceae	1	-0.0109	-0.0043	-0.0264	-0.0115	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085

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Sphaeromeria ruthiae	Compositae	3	-0.0189	-0.0331	-0.0550	-0.0417	0.0001	-0.0374	-0.0332	0.0187	0.1957	0.0469
*Sporobolus contractus**	Gramineae	2	0.0188	-0.0230	-0.0522	-0.0340	-0.0231	-0.0282	-0.0252	-0.0179	-0.0068	0.0665
Sporobolus cryptandrus	Gramineae	50	0.0570	0.0424	0.0237	0.1236	-0.0302	-0.1019	-0.0813	-0.0708	-0.0588	-0.0061
Stanleya pinnata	Cruciferae	2	0.0823	0.0677	-0.0303	-0.0340	-0.0142	-0.0352	-0.0308	-0.0179	-0.0139	-0.0121
Stellaria jamesiana	Caryophyllaceae	18	0.0048	-0.0822	-0.1064	-0.0712	-0.0308	0.0271	0.0497	0.3314	0.0534	0.0380
Stephanomeria exigua	Compositae	1	-0.0109	-0.0043	-0.0264	-0.0115	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Stephanomeria runcinata‡*	Compositae	2	0.0315	0.0213	-0.0105	-0.0144	-0.0153	-0.0212	-0.0196	-0.0179	-0.0100	-0.0121
Stephanomeria tenuifolia	Compositae	51	-0.0564	-0.0310	0.0846	0.1172	0.2097	-0.0459	-0.0537	-0.0463	0.0698	-0.0371
Stipa comata	Gramineae	39	0.0881	0.1120	0.0299	0.0637	-0.0626	-0.0597	-0.0169	-0.0122	-0.0602	-0.0490
Stipa hymenoides	Gramineae	65	-0.0221	0.0813	0.0886	0.0327	-0.0549	-0.0027	-0.0408	-0.0788	-0.0721	-0.0355
Stipa lettermanii	Gramineae	12	-0.0077	-0.0631	-0.0723	-0.0170	-0.0363	0.0173	0.0911	0.2524	-0.0184	0.0318
Stipa nelsonii	Gramineae	5	0.0436	-0.0389	-0.0550	-0.0215	-0.0285	-0.0135	0.0612	0.2604	-0.0069	0.0320
Stipa neomexicana‡‡*	Gramineae	1	0.0249	0.0040	-0.0135	-0.0240	-0.0100	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Stipa pinetorum‡*	Gramineae	2	0.0411	-0.0227	-0.0200	0.0077	-0.0155	0.0865	0.0987	0.0254	-0.0139	-0.0121
Stipa speciosa	Gramineae	15	-0.0254	0.1855	0.0749	-0.0627	-0.0373	-0.0881	-0.0779	-0.0467	-0.0332	-0.0292
*Streptanthella longirostris**	Cruciferae	11	-0.0200	0.1109	0.1070	0.0203	0.0009	-0.0483	-0.0412	-0.0386	-0.0243	-0.0234
Streptanthus cordatus	Cruciferae	38	-0.0361	0.0388	0.1502	-0.0189	-0.0797	0.0734	0.0374	-0.0617	-0.0623	-0.0533
Streptopus amplexifolius‡*	Liliaceae	1	-0.0109	0.0045	0.0285	-0.0112	-0.0104	-0.0023	-0.0037	-0.0127	-0.0098	-0.0085
*Swertia albomarginata**	Gentianaceae	11	-0.0219	0.1751	0.0796	-0.0462	-0.0533	-0.0511	-0.0527	-0.0428	-0.0330	-0.0289
Swertia radiata	Gentianaceae	11	-0.0245	-0.0538	-0.0337	-0.0212	-0.0251	0.1911	0.1982	0.0332	-0.0213	-0.0289
Swertia utahensis‡*	Gentianaceae	2	-0.0154	0.0028	-0.0200	-0.0045	-0.0140	-0.0212	-0.0196	-0.0179	-0.0139	-0.0121
Symphoricarpos oreophilus	Caprifoliaceae	58	-0.0154	-0.1199	-0.0154	-0.0492	-0.0478	0.1381	0.1700	0.2005	-0.0018	-0.0198
*Talinum parviflorum**	Portulacaceae	1	-0.0109	-0.0111	-0.0142	0.1325	0.0441	-0.0033	-0.0045	-0.0055	-0.0098	-0.0085
Tamarix chinensis€	Tamaricaceae	5	-0.0245	-0.0253	-0.0696	-0.0476	-0.0322	-0.0559	-0.0489	0.0066	0.0266	0.4269
Taraxacum officinale€	Compositae	11	0.0097	-0.0636	-0.0846	-0.0492	0.0331	-0.0170	-0.0108	0.2013	0.2364	0.1004
Tetradymia canescens	Compositae	9	-0.0062	-0.0212	0.0466	0.0890	-0.0134	-0.0331	0.0013	-0.0027	-0.0185	-0.0260
Thalictrum fendleri	Ranunculaceae	12	-0.0057	-0.0697	-0.0848	-0.0473	0.0290	0.0072	-0.0048	0.1990	0.2305	0.0461
*Thelypodium laxiflorum**	Cruciferae	7	-0.0291	-0.0363	0.0363	-0.0046	0.0139	-0.0327	-0.0249	0.0083	0.1166	0.0474
Thermopsis montana	Leguminosae	4	-0.0219	-0.0411	-0.0546	-0.0139	-0.0028	0.0401	0.0435	0.0581	0.0169	0.0308
*Thysanocarpus curvipes**	Cruciferae	10	-0.0252	0.0346	0.0630	0.0645	0.0103	-0.0466	-0.0401	-0.0296	-0.0253	-0.0116
*Townsendia incana**	Compositae	1	-0.0109	0.0220	-0.0290	-0.0240	-0.0163	-0.0248	-0.0098	-0.0127	-0.0098	0.0144

Scientific Name	Family	#Occ.	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Townsendia montana*‡‡‡	Compositae	1	-0.0109	-0.0106	0.0414	0.1042	-0.0083	-0.0248	-0.0119	0.0007	-0.0098	-0.0085
Toxicodendron rydbergii	Anacardiaceae	2	-0.0154	-0.0260	-0.0414	-0.0340	-0.0108	-0.0053	-0.0030	0.0161	0.1317	0.0538
Tradescantia occidentalis	Commelinaceae	22	-0.0477	0.0149	0.0578	0.2178	-0.0173	-0.0627	-0.0540	-0.0375	-0.0429	-0.0383
Tragopogon dubius€	Compositae	8	0.2444	-0.0352	-0.0837	-0.0421	-0.0323	-0.0355	0.0085	0.0961	-0.0101	0.0077
Tribulus terrestris€	Zygophyllaceae	2	0.1011	-0.0230	-0.0522	-0.0290	-0.0196	-0.0352	-0.0308	-0.0179	-0.0068	0.0310
Trifolium longipes	Leguminosae	10	-0.0014	-0.0608	-0.0552	0.0103	0.2031	-0.0044	0.0434	0.0456	0.0265	0.0045
Trifolium sp.	Leguminosae	2	-0.0154	-0.0161	-0.0072	-0.0228	-0.0196	-0.0282	-0.0167	0.0097	0.0194	0.2472
Typha latifolia	Typhaceae	1	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	0.0122	0.0117	0.1572
Valeriana occidentalis*‡‡‡	Valerianaceae	1	-0.0109	-0.0204	-0.0217	-0.0092	0.1027	0.0191	0.0034	-0.0127	0.0353	-0.0085
Verbascum thapsus€	Scrophulariaceae	5	-0.0103	-0.0370	-0.0698	-0.0372	-0.0105	-0.0340	-0.0374	0.1451	0.1323	0.3743
Vicia americana	Leguminosae	43	-0.0117	-0.0951	-0.0621	-0.0652	-0.0499	0.0806	0.1074	0.2497	0.0347	0.0130
Vicia ludoviciana*	Leguminosae	1	0.0196	0.0550	-0.0107	-0.0177	-0.0163	-0.0248	-0.0217	-0.0127	-0.0098	-0.0085
Viguiera multiflora	Compositae	12	0.0440	-0.0363	-0.0190	-0.0051	-0.0318	0.0174	0.0916	0.0675	-0.0243	-0.0212
Viola canadensis*	Violaceae	5	-0.0245	-0.0441	-0.0655	-0.0388	0.0225	-0.0120	-0.0347	0.0734	0.3300	0.0892
Viola nuttallii*‡	Violaceae	1	-0.0109	-0.0133	-0.0368	-0.0149	-0.0163	-0.0150	-0.0040	0.0934	0.0023	0.0255
Viola purpurea	Violaceae	10	0.0039	-0.0474	-0.0220	-0.0334	-0.0446	0.2702	0.1282	-0.0322	-0.0314	-0.0275
Vitis arizonica	Vitaceae	1	-0.0109	-0.0162	-0.0290	-0.0240	-0.0163	-0.0150	-0.0138	0.0136	0.1491	0.0709
Woodsia oregana*	Polypodiaceae	1	-0.0109	-0.0162	0.0052	0.0023	0.0567	0.0140	-0.0138	-0.0004	0.0878	-0.0085
Wyethia arizonica	Compositae	5	-0.0245	-0.0350	-0.0428	0.0301	0.1696	-0.0313	-0.0292	-0.0253	-0.0192	-0.0192
Xanthium strumarium*	Compositae	1	-0.0109	-0.0117	-0.0232	-0.0169	-0.0113	-0.0248	-0.0217	0.0263	0.0371	0.3576
Yucca angustissima[4]	Agavaceae	41	-0.0660	-0.0505	0.1162	0.1379	0.0550	-0.0337	-0.0226	-0.0629	-0.0344	-0.0521
Yucca baccata	Agavaceae	17	-0.0066	0.1913	0.0981	-0.0227	-0.0344	-0.0682	-0.0588	-0.0489	-0.0392	-0.0318
Zauschneria latifolia	Onagraceae	15	-0.0160	-0.0558	-0.0283	0.0005	0.2515	-0.0038	-0.0293	0.0217	0.1956	-0.0039
Zigadenus paniculatus*	Liliaceae	12	0.1141	-0.0079	-0.0120	-0.0498	-0.0432	0.0843	0.1945	-0.0016	-0.0320	-0.0302

*not recorded by the USGS-NPS vegetation survey at Zion N.P. (Cogan et al. 2004)
‡not mentioned in the Zion N.P. annotated checklist (Fertig and Alexander 2009)
‡‡mentioned as unconfirmed in the Zion N.P. annotated checklist (Fertig and Alexander 2009)
‡‡‡ mentioned as falsely reported or questionable in the Zion N.P. annotated checklist (Fertig and Alexander 2009)
€ exotic taxa (Welsh et al. 2003, Fertig and Alexander 2009)
[1] Probably equivalent to *Artemisia nova* in Cogan et al. 2004; described as *A. nova* var. *arbuscula* in Fertig and Alexander 2009
[2] Probably equivalent to *Elymus lanceolatus* as well as *Pascopyrum smithii* in Cogan et al. 2004
[3] Includes *Gutierrezia microcephala* and *G. sarothrae*
[4] Probably equivalent to *Yucca elata* var. *utahensis* in Cogan et al. 2004

APPENDIX 2.3

Modal species of vegetation types described by Harper et al. (2001) for Zion National Park, Utah (rows) and their affinities to coalition species groups of the current study (columns). Following Curtis (1959), modal species are prevalent (frequently-occurring) species assigned to the vegetation type where their percent occurrence is highest. Affinities are mean pairwise association values (in units of the phi coefficient) between a species and members of a coalition group. Species are listed in descending order of percent occurrence (percent of plots of indicated vegetation plot where species was recorded). See Table 2.3 for mean affinity values by vegetation type.

Vegetation Type	Species	% Occ	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Abandoned Fields	*Bromus tectorum*	100	0.1156	0.2135	0.0710	-0.0590	-0.1214	-0.1832	-0.1512	-0.1083	-0.0873	0.0262
Abandoned Fields	*Chamaesyce albomarginata*	67	0.2085	0.0081	-0.0514	-0.0601	-0.0683	0.0486	0.0045	-0.0518	-0.0427	-0.0065
Abandoned Fields	*Sporobolus cryptandrus*	67	0.0570	0.0424	0.0237	0.1236	-0.0302	-0.1019	-0.0813	-0.0708	-0.0588	-0.0061
Abandoned Fields	*Tragopogon dubius*	67	0.2444	-0.0352	-0.0837	-0.0421	-0.0323	-0.0355	0.0085	0.0961	-0.0101	0.0077
Abandoned Fields	*Erodium cicutarium*	50	0.2865	0.1277	-0.0910	-0.0748	-0.0488	-0.0766	-0.0609	-0.0407	-0.0282	-0.0211
Abandoned Fields	*Lactuca serriola*	50	0.2237	-0.0045	-0.0836	-0.0662	-0.0233	-0.0521	-0.0387	0.0166	0.0243	0.0185
Abandoned Fields	*Astragalus nuttallianus*	40	0.0317	0.2167	-0.0609	-0.0709	-0.0475	-0.0755	-0.0594	-0.0385	-0.0297	-0.0260
Abandoned Fields	*Aristida purpurea*	33	0.0216	0.1291	0.0011	-0.0051	-0.0026	-0.0986	-0.0888	-0.0646	-0.0393	0.0031
Abandoned Fields	*Artemisia dracunculus*	33	0.0695	-0.0227	-0.0022	-0.0069	-0.0291	-0.0208	-0.0178	-0.0225	-0.0260	-0.0138
Abandoned Fields	*Atriplex canescens*	33	0.2722	0.0716	-0.0649	-0.0708	-0.0447	-0.0797	-0.0634	-0.0407	-0.0314	-0.0275
Abandoned Fields	*Lycium pallidum*	33	0.3355	0.0067	-0.0506	-0.0376	-0.0255	-0.0431	-0.0263	-0.0220	-0.0170	-0.0149
Abandoned Fields	*Sphaeralcea grossulariifolia*	33	0.2053	0.0710	-0.0075	-0.0691	-0.0565	-0.0771	-0.0643	-0.0423	-0.0347	-0.0224
Blackbrush	*Coleogyne ramosissima*	100	0.0145	0.2448	-0.0393	-0.0830	-0.0601	-0.0914	-0.0800	-0.0466	-0.0360	-0.0315
Blackbrush	*Gilia inconspicua*	90	-0.0137	0.2558	0.1513	0.0515	-0.1029	-0.1116	-0.0963	-0.1140	-0.0969	-0.0584
Blackbrush	*Bromus rubens*	80	0.0339	0.3680	0.0731	-0.0990	-0.0855	-0.1439	-0.1239	-0.0865	-0.0642	-0.0544
Blackbrush	*Gutierrezia microcephala*[1]	80	0.0989	0.2817	0.0670	-0.0696	-0.0984	-0.1590	-0.1114	-0.1043	-0.0962	-0.0086
Blackbrush	*Festuca octoflora*	70	0.0169	0.2480	0.0657	0.0993	-0.0069	-0.1467	-0.1123	-0.0946	-0.0819	-0.0469
Blackbrush	*Hilaria* sp.	60	0.1280	0.2507	0.0402	-0.1195	-0.0871	-0.1262	-0.1138	-0.0683	-0.0675	-0.0510

Vegetation Type	Species	% Occ	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Blackbrush (cont.)	*Cryptantha* sp. (annual)	50	-0.0026	0.2085	0.1317	0.0211	-0.0596	-0.1192	-0.0796	-0.0746	-0.0776	-0.0639
Blackbrush	*Draba verna*	50	0.0217	0.2595	0.0867	-0.0141	-0.0704	-0.0816	-0.0745	-0.0737	-0.0615	-0.0189
Blackbrush	*Eriogonum palmerianum*	50	0.0092	0.2175	0.0316	-0.0719	-0.0476	-0.0797	-0.0779	-0.0503	-0.0369	-0.0339
Blackbrush	*Calochortus flexuosus*	40	0.0171	0.1303	-0.0365	-0.0562	-0.0395	-0.0626	-0.0550	-0.0302	-0.0261	-0.0160
Blackbrush	*Descurainia pinnata*	40	-0.0037	0.1716	0.0713	-0.0494	-0.0819	-0.0556	-0.0588	0.0116	-0.0520	-0.0214
Blackbrush	*Ephedra nevadensis*	40	0.0478	0.2637	0.0091	-0.0872	-0.0630	-0.0888	-0.0854	-0.0554	-0.0394	-0.0374
Blackbrush	*Stipa hymenoides*	40	-0.0221	0.0813	0.0886	0.0327	-0.0549	-0.0027	-0.0408	-0.0788	-0.0721	-0.0355
Blackbrush	*Oenothera pallida*	33	-0.0224	0.0081	0.0494	0.1056	-0.0116	-0.0433	-0.0436	-0.0284	-0.0092	0.1363
Blackbrush	*Eriastrum eremicum*	30	-0.0062	0.2058	0.0095	-0.0395	-0.0417	-0.0626	-0.0550	-0.0339	-0.0261	-0.0229
Blackbrush	*Poa bigelovii*	30	0.0487	0.1065	-0.0240	-0.0542	-0.0388	-0.0675	-0.0593	-0.0329	-0.0280	-0.0181
Blackbrush	*Psorothamnus fremontii*	30	0.0240	0.2031	-0.0107	-0.0679	-0.0532	-0.0747	-0.0660	-0.0428	-0.0330	-0.0289
Sagebrush	*Artemisia tridentata*	100	0.0211	0.0237	0.0140	0.0087	-0.0941	-0.0650	-0.0307	-0.0021	-0.0710	-0.0200
Sagebrush	*Gutierrezia sarothrae*[1]	71	0.0989	0.2817	0.0670	-0.0696	-0.0984	-0.1590	-0.1114	-0.1043	-0.0962	-0.0086
Sagebrush	*Elymus elymoides*	57	0.0162	0.0923	0.0099	0.0133	0.0141	-0.0536	-0.0274	-0.0206	-0.0247	-0.0314
Sagebrush	*Chrysothamnus nauseosus*	43	-0.0081	0.0136	0.0303	0.1202	-0.0282	-0.0941	-0.0726	-0.0711	-0.0435	0.0411
Sagebrush	*Eriastrum sparsiflorum*	29	0.0561	0.1752	-0.0212	-0.0568	-0.0495	-0.0914	-0.0710	-0.0466	-0.0360	-0.0250
Sagebrush	*Erigeron divergens*	29	-0.0097	-0.0041	0.0203	-0.0308	-0.0587	-0.0115	0.0173	0.0552	-0.0393	-0.0170
Sagebrush	*Opuntia phaeacantha*	29	0.1030	0.0449	0.0187	0.0060	-0.0339	-0.0589	-0.0420	-0.0291	-0.0297	-0.0200
Sagebrush	*Pectocarya setosa*	29	0.0226	0.0666	-0.0321	-0.0339	-0.0255	-0.0431	-0.0263	-0.0220	-0.0170	-0.0149
Juniper-Pinyon	*Juniperus osteosperma*	82	0.0251	0.1706	0.1868	-0.0462	-0.1486	0.0226	0.0318	-0.1258	-0.1273	-0.1076
Juniper-Pinyon	*Amelanchier utahensis*	65	-0.0900	-0.0968	0.1661	0.0340	-0.0081	0.1990	0.1598	-0.0446	-0.0817	-0.1249
Juniper-Pinyon	*Arabis perennans*	57	-0.0953	0.0295	0.2379	0.0173	0.0178	0.0472	0.0240	-0.0499	-0.0301	-0.0931
Juniper-Pinyon	*Pinus monophylla*	53	-0.0639	0.1617	0.1964	-0.0616	-0.1071	-0.1054	-0.0930	-0.0808	-0.0790	-0.0597
Juniper-Pinyon	*Pinus edulis*	34	-0.0363	-0.0799	0.0969	0.0150	-0.0519	0.2160	0.1513	-0.0540	-0.0481	-0.0640
Juniper-Pinyon	*Streptanthus cordatus*	31	-0.0361	0.0388	0.1502	-0.0189	-0.0797	0.0734	0.0374	-0.0617	-0.0623	-0.0533
Juniper-Pinyon	*Erigeron sionis*	29	-0.0219	-0.0387	-0.0358	0.0211	0.2217	0.0074	-0.0145	0.0187	0.1662	0.0426
Mountain Brush	*Eriogonum racemosum*	33	-0.0291	-0.0898	0.0990	0.1001	0.0704	-0.0038	0.0302	0.0394	0.0517	-0.0253
Mountain Brush	*Erysimum asperum*	32	-0.0775	-0.0340	0.2064	0.1601	-0.0076	0.0100	0.0369	-0.0315	-0.0287	-0.0527
Mountain Brush	*Machaeranthera canescens*	32	-0.0036	0.0284	0.0883	0.1432	-0.0142	-0.0414	-0.0210	-0.0066	-0.0534	-0.0318
Mountain Brush	*Phacelia heterophylla*	32	-0.0498	-0.0651	0.0028	0.0973	0.0148	-0.0231	-0.0256	0.1026	0.0676	0.1188

Vegetation Type	Species	% Occ	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Rock Crevice	*Cercocarpus intricatus*	84	-0.0741	-0.0732	-0.0008	0.0948	0.3022	-0.0254	-0.0425	-0.0540	0.0241	-0.0535
Rock Crevice	*Arenaria fendleri*	64	-0.0544	-0.0513	-0.0408	0.1880	0.2407	-0.0605	-0.0522	-0.0512	-0.0203	-0.0427
Rock Crevice	*Chrysopsis villosa*	64	-0.0433	-0.0529	0.0206	0.1933	0.1966	-0.0952	-0.0770	-0.0592	0.0364	0.0487
Rock Crevice	*Castilleja scabrida*	60	-0.0392	-0.0544	-0.0185	0.0831	0.2903	-0.0401	-0.0609	-0.0449	0.0430	-0.0458
Rock Crevice	*Opuntia macrorhiza*	56	-0.0871	0.0051	0.1969	0.2100	0.0551	0.0113	0.0278	-0.0893	-0.0880	-0.1079
Rock Crevice	*Stephanomeria tenuifolia*	48	-0.0564	-0.0310	0.0846	0.1172	0.2097	-0.0459	-0.0537	-0.0463	0.0698	-0.0371
Rock Crevice	*Penstemon laevis*	40	-0.0532	-0.0162	0.0773	0.2316	0.0846	-0.0416	-0.0335	-0.0542	-0.0342	-0.0456
Rock Crevice	*Chaenactis douglasii*	36	-0.0625	-0.0719	0.1114	0.2527	0.1140	-0.0008	0.0032	-0.0622	-0.0409	-0.0586
Rock Crevice	*Cryptantha confertiflora*	36	-0.0351	0.0704	0.1252	0.0887	0.0972	-0.0691	-0.0637	-0.0683	-0.0403	-0.0469
Rock Crevice	*Penstemon humilis*	36	-0.0593	-0.0565	0.0790	0.1052	0.2021	-0.0007	-0.0125	-0.0374	0.0411	-0.0438
Rock Crevice	*Quercus turbinella*	32	-0.0617	0.1136	0.2131	0.0456	-0.0280	-0.0980	-0.0825	-0.0805	-0.0597	-0.0524
Rock Crevice	*Erigeron canaani*	28	-0.0448	-0.0719	-0.0209	0.1198	0.2338	0.0168	-0.0131	-0.0192	0.0259	-0.0316
Rock Crevice	*Penstemon rostriflorus*	28	-0.0179	-0.0415	0.0496	-0.0137	0.1297	0.0101	-0.0091	0.0460	0.1111	-0.0184
Ponderosa Pine	*Pinus ponderosa*	97	-0.0574	-0.1236	-0.0675	0.1735	0.1993	0.0611	0.0717	-0.0050	0.0285	-0.0322
Ponderosa Pine	*Poa fendleriana*	85	-0.1391	-0.0620	0.2132	0.1283	0.1186	0.0577	0.0891	-0.0417	-0.0072	-0.0837
Ponderosa Pine	*Arctostaphylos patula*	61	-0.1013	-0.0593	0.1132	0.2147	0.0767	0.0893	0.0301	-0.0959	-0.0837	-0.0949
Ponderosa Pine	*Senecio multilobatus*	52	-0.0802	-0.1087	0.1615	0.1919	0.1136	0.0662	0.0478	-0.0288	-0.0054	-0.0606
Ponderosa Pine	*Phlox austromontana*	39	-0.0767	-0.0520	0.1251	0.1886	0.0721	0.0491	0.0433	-0.0512	-0.0503	-0.0675
Ponderosa Pine	*Polygonum douglasii*	33	-0.0015	-0.0693	-0.0321	0.1548	0.0311	0.0050	0.0855	0.1711	-0.0403	-0.0010
Ponderosa Pine	*Purshia tridentata*	30	-0.0398	-0.0642	0.0241	0.0959	-0.0355	0.1318	0.1832	-0.0297	-0.0563	-0.0475
Ponderosa Pine	*Arenaria macradenia*	24	-0.0804	-0.0607	0.1271	0.0990	0.1502	-0.0052	-0.0069	-0.0401	-0.0037	-0.0588
Ponderosa Pine	*Comandra umbellata*	24	-0.0686	-0.0696	0.0777	0.1314	0.0282	0.0257	0.0821	-0.0146	-0.0470	-0.0505
Ponderosa Pine	*Yucca angustissima*	24	-0.0660	-0.0505	0.1162	0.1379	0.0550	-0.0337	-0.0226	-0.0629	-0.0344	-0.0521
Douglas Fir-White Fir	*Quercus gambelii*	86	-0.0835	-0.2123	-0.0259	0.0354	0.0422	0.1792	0.1804	0.1418	0.0666	-0.0480
Douglas Fir-White Fir	*Pachystima myrsinites*	71	-0.0573	-0.1407	-0.0118	0.0118	0.0706	0.2096	0.1310	0.0248	0.1121	-0.0386
Douglas Fir-White Fir	*Carex rossii*	57	-0.0335	-0.1431	-0.0482	0.0505	0.1222	0.2114	0.1553	0.1027	0.0042	-0.0554
Douglas Fir-White Fir	*Abies concolor*	52	-0.0226	-0.0893	-0.0770	-0.0559	0.0865	0.0603	0.0229	0.1859	0.2236	0.0410
Douglas Fir-White Fir	*Symphoricarpos oreophilus*	52	-0.0154	-0.1199	-0.0154	-0.0492	-0.0478	0.1381	0.1700	0.2005	-0.0018	-0.0198
Douglas Fir-White Fir	*Pseudotsuga menziesii*	48	-0.0476	-0.0849	-0.0415	-0.0183	0.1328	0.0553	0.0042	0.0309	0.2559	0.0212
Douglas Fir-White Fir	*Vicia americana*	48	-0.0117	-0.0951	-0.0621	-0.0652	-0.0499	0.0806	0.1074	0.2497	0.0347	0.0130

Vegetation Type	Species	% Occ	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Douglas Fir-White Fir (cont.)	*Acer grandidentatum*	43	-0.0556	-0.0988	-0.0451	-0.0489	0.0587	0.0312	0.0003	0.1139	0.2614	0.0429
Douglas Fir-White Fir	*Draba asprella*	38	-0.0516	-0.0823	0.0124	0.0971	0.2068	0.0802	0.0067	-0.0115	0.1409	-0.0142
Douglas Fir-White Fir	*Haplopappus scopulorum*	38	-0.0620	-0.0438	0.1804	0.0711	0.0046	0.0255	0.0324	-0.0509	-0.0055	-0.0515
Douglas Fir-White Fir	*Mahonia repens*	38	-0.0231	-0.0947	-0.0511	-0.0508	-0.0046	0.1614	0.0969	0.0752	0.1310	0.0000
Douglas Fir-White Fir	*Holodiscus dumosus*	33	-0.0356	-0.0921	-0.0438	0.0077	0.3078	-0.0046	-0.0308	-0.0027	0.1947	-0.0222
Douglas Fir-White Fir	*Fraxinus anomala*	29	-0.0588	0.0431	0.2408	-0.0204	0.0183	0.0824	0.0020	-0.0571	-0.0092	-0.0520
Douglas Fir-White Fir	*Heuchera rubescens*	29	-0.0292	-0.0709	-0.0461	-0.0292	0.1744	0.0382	-0.0019	0.0476	0.2533	-0.0007
Douglas Fir-White Fir	*Stellaria jamesiana*	29	0.0048	-0.0822	-0.1064	-0.0712	-0.0308	0.0271	0.0497	0.3314	0.0534	0.0380
Douglas Fir-White Fir	*Juniperus scopulorum*	24	-0.0178	-0.0775	-0.0461	-0.0170	-0.0283	0.0539	0.0409	0.1754	0.0134	0.0109
Hanging Gardens	*Adiantum capillus-veneris*	89	-0.0154	-0.0290	-0.0466	-0.0340	-0.0028	-0.0352	-0.0308	0.0132	0.1540	-0.0025
Hanging Gardens	*Calamagrostis scopulorum*	79	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	0.0179	-0.0085
Hanging Gardens	*Aster welshii*	72	-0.0269	-0.0449	-0.0609	-0.0507	-0.0144	-0.0372	-0.0375	0.0224	0.1633	0.1134
Hanging Gardens	*Lobelia cardinalis*^{2}	56	--	--	--	--	--	--	--	--	--	--
Hanging Gardens	*Aquilegia chrysantha*	50	-0.0109	-0.0204	-0.0368	-0.0240	-0.0163	-0.0248	-0.0217	-0.0127	0.0179	-0.0085
Hanging Gardens	*Aquilegia formosa*	50	-0.0189	-0.0355	-0.0509	-0.0269	0.0919	-0.0250	-0.0232	-0.0163	0.0585	-0.0070
Hanging Gardens	*Dodecatheon pulchellum*	44	-0.0154	-0.0290	-0.0469	-0.0340	-0.0108	-0.0123	-0.0086	-0.0025	0.0387	-0.0025
Hanging Gardens	*Apocynum androsaemifolium*	40	-0.0154	-0.0290	-0.0414	-0.0189	0.0270	0.0152	-0.0030	0.0476	0.2110	0.0817
Hanging Gardens	*Aster glaucodes*	40	-0.0269	-0.0144	0.0115	-0.0389	-0.0091	-0.0054	-0.0173	0.0135	0.1160	0.1156
Hanging Gardens	*Eupatorium herbaceum*	40	-0.0081	-0.0709	-0.0670	-0.0391	0.1492	0.0054	-0.0365	0.0630	0.3612	0.0462
Hanging Gardens	*Solidago velutina*	40	0.0085	-0.1190	-0.0889	0.0046	0.1890	0.0614	0.1036	0.0889	0.1476	-0.0134
Hanging Gardens	*Erigeron utahensis*	39	-0.0341	0.1342	0.2246	0.0464	-0.0274	-0.0700	-0.0681	-0.0713	-0.0588	-0.0560
Hanging Gardens	*Petrophytum caespitosum*	39	-0.0385	-0.0612	-0.0582	0.0268	0.3143	0.0020	-0.0243	-0.0130	0.1274	0.0088
Hanging Gardens	*Muhlenbergia thurberi*	33	-0.0174	-0.0610	-0.0526	0.0809	0.2838	-0.0207	-0.0274	-0.0274	0.0811	-0.0182
Hanging Gardens	*Smilacina stellata*	33	-0.0189	-0.0355	-0.0640	-0.0334	-0.0215	0.0102	-0.0142	0.0284	0.0379	-0.0060
Hanging Gardens	*Agrostis stolonifera*	28	-0.0109	-0.0183	-0.0329	-0.0240	-0.0163	-0.0248	-0.0217	0.0068	0.0093	0.2268
Hanging Gardens	*Carex curatorum*^{2}	28	--	--	--	--	--	--	--	--	--	--
Hanging Gardens	*Cirsium arizonicum*	26	0.0236	-0.0538	0.0075	0.0434	0.1052	0.0028	-0.0078	0.0262	0.0954	0.0911
Hanging Gardens	*Antennaria rosulata*	20	-0.0189	-0.0276	-0.0021	-0.0057	0.0238	0.0195	0.0148	0.0635	0.1447	0.0540

Vegetation Type	Species	% Occ	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Riparian	*Mimulus cardinalis*	72	-0.0154	-0.0260	-0.0466	-0.0340	-0.0231	-0.0282	-0.0252	0.0007	0.1183	0.0442
Riparian	*Acer negundo*	63	-0.0226	-0.0711	-0.0929	-0.0678	0.0736	-0.0447	-0.0579	0.0499	0.3163	0.2513
Riparian	*Artemisia ludoviciana*	42	-0.0089	0.0007	0.1161	0.0261	0.0346	-0.0376	-0.0201	0.0195	0.0962	0.1026
Riparian	*Bromus diandrus*	42	0.0312	-0.0336	-0.0857	-0.0613	-0.0407	-0.0734	-0.0647	-0.0126	0.0071	0.3353
Riparian	*Bromus ciliatus*	37	0.0293	-0.0670	-0.0665	-0.0486	0.0757	-0.0176	-0.0460	0.0473	0.2602	0.0995
Riparian	*Senecio spartioides*	37	-0.0242	-0.0684	-0.0308	0.0456	0.0257	-0.0538	-0.0629	0.0085	0.1054	0.0200
Riparian	*Fraxinus velutina*	32	-0.0169	-0.0349	-0.0638	-0.0478	-0.0313	-0.0546	-0.0496	-0.0130	0.0263	0.1862
Riparian	*Populus fremontii*	32	-0.0139	-0.0177	-0.0756	-0.0534	-0.0362	-0.0613	-0.0487	0.0008	0.0149	0.3936
Riparian	*Equisetum hyemale*	26	0.0242	-0.0422	-0.0812	-0.0464	-0.0190	-0.0501	-0.0537	0.0372	0.1603	0.3744
Riparian	*Zauschneria latifolia*	26	-0.0160	-0.0558	-0.0283	0.0005	0.2515	-0.0038	-0.0293	0.0217	0.1956	-0.0039
Riparian	*Cystopteris fragilis*	21	0.0155	-0.0505	-0.0547	-0.0311	0.0833	-0.0160	-0.0366	0.0764	0.3184	0.0691
Riparian	*Poa pratensis*	21	-0.0045	-0.0598	-0.0991	-0.0276	-0.0409	-0.0455	-0.0258	0.2466	0.0391	0.2027
Riparian	*Tamarix chinensis*	21	-0.0245	-0.0253	-0.0696	-0.0476	-0.0322	-0.0559	-0.0489	0.0066	0.0266	0.4269
Riparian	*Thelypodium laxiflorum*	21	-0.0291	-0.0363	0.0363	-0.0046	0.0139	-0.0327	-0.0249	0.0083	0.1166	0.0474

[1] The species of *Gutierrezia* listed in Harper et al. (2001) were lumped in the current analysis due to identification uncertainties

[2] *Carex curatorum* and *Lobelia cardinalis* were listed in Harper et al. (2001) due to their inclusion of supplemental hanging garden data not used in the current analysis

APPENDIX 2.4

U.S. National Vegetation Classification System (NVCS) associations of Zion National Park, Utah as recognized by Cogan et al. (2004) (rows) with their compositional affinities to coalition species groups of the current study (columns). Affinity values are in units of the phi coefficient, calculated for each species in relation to each coalition group (see Appendix 2.2) and then averaged across associations in proportion to their species frequencies. Low values (green shading) indicate low correspondence between associations and coalition groups; high values (red shading) indicate high correspondence (shading is scaled separately for each column). Associations are grouped by physiognomic class and alliance; see also Table 2.4. Note that association names are truncated omitting physiognomic descriptors.

	Cluster[1]	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
I. FOREST											
White Fir Forest Alliance											
White Fir / Bigtooth Maple	CrvcC/HPltu	-0.0367	-0.0767	-0.0156	-0.0019	0.0521	0.0524	0.0347	0.0785	0.1288	0.0213
White Fir / Gambel Oak	CrvcC/HPltu	-0.0408	-0.0982	-0.0198	-0.0006	0.0440	0.0957	0.0788	0.1057	0.0897	-0.0068
White Fir / Greenleaf Manzanita	MsaTp	-0.0442	-0.0862	0.0015	0.0176	0.0408	0.1158	0.0961	0.0639	0.0486	-0.0254
White Fir / Mountain Snowberry	HPltu	-0.0206	-0.0714	-0.0223	-0.0081	0.0001	0.0594	0.0731	0.1542	0.0412	0.0061
Douglas-fir Forest Alliance											
Douglas-fir / Bigtooth Maple	CrvcC	-0.0368	-0.0773	-0.0487	-0.0182	0.0594	0.0435	0.0067	0.0481	0.1910	0.0634
Douglas-fir / Gambel Oak	CrvcC/HPltu	-0.0461	-0.0697	0.0161	0.0117	0.0477	0.0662	0.0436	0.0487	0.0855	-0.0095
Douglas-fir / Mountain Snowberry	CrvcC/HPltu	-0.0345	-0.0557	0.0114	0.0082	0.0298	0.0635	0.0536	0.0520	0.0551	0.0000
Bigtooth Maple Montane Forest Alliance											
Bigtooth Maple / Gambel Oak	CrvcC/HPltu	-0.0266	-0.0669	-0.0086	0.0090	0.0228	0.0316	0.0282	0.0782	0.0703	0.0274
Quaking Aspen Forest Alliance											
Quaking Aspen / Mountain Snowberry / Tall Forbs	HPltu	-0.0067	-0.0594	-0.0505	-0.0256	-0.0049	0.0256	0.0391	0.1860	0.0609	0.0457
Quaking Aspen Temporarily Flooded Forest Alliance											
Quaking Aspen / Gambel Oak / Mountain Snowberry	HPltu	0.0108	-0.0644	-0.0556	-0.0237	0.0001	0.0270	0.0497	0.1635	0.0604	0.0600
Fremont Cottonwood Temporarily Flooded Forest Alliance											
Fremont Cottonwood / Coyote Willow	Strmb	0.0077	0.0214	-0.0014	-0.0056	-0.0186	-0.0471	-0.0381	-0.0114	0.0069	0.1520
White Fir - Quaking Aspen Forest Alliance											
Quaking Aspen - White Fir / Kentucky Bluegrass Semi-natural	HPltu	0.0062	-0.0447	-0.0404	-0.0046	0.0024	0.0100	0.0221	0.1285	0.0457	0.0400
Quaking Aspen - White Fir / Mountain Snowberry	HPltu	-0.0183	-0.0708	-0.0318	-0.0087	0.0165	0.0517	0.0589	0.1266	0.0659	0.0104

	Cluster[1]	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
II. WOODLAND											
Two-needle Pinyon - (Juniper species) Woodland Alliance											
Two-needle Pinyon - Juniper species / Big Sagebrush	UpSnd/RckSl	-0.0224	0.0012	0.0675	0.0806	-0.0180	0.0112	0.0186	-0.0387	-0.0479	-0.0470
Two-needle Pinyon - Juniper species / Gambel Oak	MsaTp/RckSl	-0.0449	-0.0447	0.0714	0.0486	0.0052	0.0814	0.0761	-0.0107	-0.0215	-0.0477
Two-needle Pinyon - Juniper species / Mountain-mahogany	MsaTp/RckSl	-0.0374	-0.0230	0.0898	0.0229	-0.0176	0.1039	0.0808	-0.0317	-0.0461	-0.0622
Two-needle Pinyon - Utah Juniper / Greenleaf Manzanita	MsaTp/RckSl	-0.0542	-0.0407	0.0953	0.0627	0.0079	0.0983	0.0780	-0.0313	-0.0351	-0.0663
Two-needle Pinyon - Utah Juniper / Littleleaf Mtn-mahogany	UpSnd/RckSl	-0.0395	0.0053	0.1013	0.0582	0.0180	0.0221	0.0184	-0.0448	-0.0344	-0.0436
Two-needle Pinyon - Utah Juniper / Stansbury Cliff-rose	MsaTp/RckSl	-0.0407	0.0065	0.0965	0.0272	-0.0123	0.0577	0.0410	-0.0386	-0.0391	-0.0528
Two-needle Pinyon / Curl-leaf Mountain-mahogany	MsaTp	-0.0329	-0.0587	0.0439	0.0305	-0.0002	0.0817	0.0847	0.0195	-0.0217	-0.0407
Ponderosa Pine Woodland Alliance											
Ponderosa Pine / Black Sagebrush	MsaTp	-0.0296	-0.0548	0.0250	0.0294	0.0106	0.0564	0.0747	0.0357	-0.0105	-0.0261
Ponderosa Pine / Gambel Oak	MsaTp	-0.0295	-0.0601	0.0136	0.0478	0.0331	0.0531	0.0639	0.0427	0.0121	-0.0214
Ponderosa Pine / Greenleaf Manzanita	MsaTp/RckSl	-0.0408	-0.0507	0.0357	0.0660	0.0309	0.0768	0.0651	-0.0049	-0.0160	-0.0431
Ponderosa Pine / Northern Bracken	CrvcC/HPltu	-0.0297	-0.0532	-0.0254	0.0398	0.0498	0.0049	0.0077	0.0707	0.0378	0.0218
Ponderosa Pine / Smooth Brome Semi-natural	CrvcC/HPltu	-0.0197	-0.0553	-0.0214	0.0371	0.0429	0.0145	0.0337	0.0901	0.0337	0.0368
Utah Juniper Woodland Alliance											
Utah Juniper / Big Sagebrush	ArdLw	0.0212	0.1489	0.0947	0.0031	-0.0698	-0.0558	-0.0336	-0.0754	-0.0844	-0.0563
Singleleaf Pinyon - (Utah Juniper) Woodland Alliance											
Singleleaf Pinyon - Utah Juniper / (Rd. Buffalob., Ut. Serviceb.)	RckSl	-0.0236	0.0722	0.1224	0.0204	-0.0195	-0.0223	-0.0156	-0.0549	-0.0480	-0.0474
Singleleaf Pinyon - Utah Juniper / Big Sagebrush	ArdLw	0.0131	0.1264	0.0825	-0.0170	-0.0564	-0.0555	-0.0398	-0.0604	-0.0604	-0.0389
Singleleaf Pinyon - Utah Juniper / Black Sagebrush	RckSl	-0.0010	0.0719	0.0775	-0.0188	-0.0448	-0.0180	0.0019	-0.0356	-0.0543	-0.0459
Singleleaf Pinyon - Utah Juniper / Blackbrush	ArdLw	0.0036	0.1322	0.0856	-0.0079	-0.0693	-0.0479	-0.0263	-0.0647	-0.0696	-0.0471
Singleleaf Pinyon - Utah Juniper / Mtn-mahogany - Gambel Oak	MsaTp/RckSl	-0.0517	-0.0051	0.1151	0.0158	-0.0391	0.0742	0.0598	-0.0393	-0.0561	-0.0758
Singleleaf Pinyon - Utah Juniper / Sparse Understory	RckSl	-0.0152	0.0704	0.1077	0.0154	-0.0413	-0.0129	-0.0002	-0.0555	-0.0598	-0.0531
Singleleaf Pinyon - Utah Juniper / Turbinella Live Oak	RckSl	-0.0164	0.0753	0.1121	0.0272	-0.0245	-0.0365	-0.0259	-0.0569	-0.0490	-0.0373
Rocky Mountain Juniper Woodland Alliance											
Rocky Mountain Juniper - Gambel Oak	--	-0.0309	-0.0325	0.0252	0.0206	0.0073	0.0133	0.0170	0.0282	0.0380	0.0585
Box-elder Temporarily Flooded Woodland Alliance											
Box-elder / Disturbed Understory	Strmb/HPltu	0.0062	-0.0197	-0.0053	0.0110	-0.0027	-0.0242	-0.0165	0.0434	0.0480	0.0505
Box-elder / Tasselflower Brickelbush	CrvcC	-0.0029	-0.0499	-0.0443	-0.0152	0.0506	-0.0146	-0.0206	0.0869	0.1435	0.0664

	Cluster[1]	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
II. WOODLAND (cont.)											
Fremont Cottonwood Temporarily Flooded Woodland Alliance											
Fremont Cottonwood - Velvet Ash	Strmb	-0.0040	-0.0014	-0.0135	-0.0234	-0.0161	-0.0414	-0.0400	-0.0128	0.0370	0.1710
Fremont Cottonwood / Emory Seepwillow	Strmb	-0.0036	0.0135	0.0023	0.0057	-0.0152	-0.0474	-0.0355	-0.0098	0.0046	0.1466
Single-leaf Ash Temporarily Flooded Woodland Alliance											
Single-leaf Ash	RckSl	-0.0310	0.0288	0.0902	0.0149	-0.0133	-0.0076	-0.0074	-0.0109	-0.0067	-0.0141
III. SHRUBLAND											
Greenleaf Manzanita Shrubland Alliance											
Greenleaf Manzanita - Gambel Oak - (Ut. Serviceberry)	MsaTp/RckSl	-0.0488	-0.0501	0.0729	0.0715	0.0263	0.0718	0.0665	-0.0080	-0.0201	-0.0521
Greenleaf Manzanita - Mountain Big Sagebrush	UpSnd	-0.0460	-0.0387	0.0579	0.1264	0.0219	0.0062	0.0230	-0.0183	-0.0314	-0.0416
Greenleaf Manzanita	UpSnd/RckSl	-0.0444	-0.0437	0.0560	0.0912	0.0425	0.0383	0.0363	-0.0125	-0.0169	-0.0399
Mexican Manzanita Shrubland Alliance											
Mexican Manzanita	MsaTp	-0.0425	-0.0717	0.0225	0.0303	0.0317	0.0921	0.0651	0.0242	0.0246	0.0039
Turbinella Live Oak Shrubland Alliance											
Turbinella Live Oak - (Utah Serviceberry) Colluvial	RckSl	-0.0223	0.0281	0.0948	0.0332	-0.0017	-0.0055	-0.0012	-0.0287	-0.0253	-0.0274
Arrow-weed Seasonally Flooded Shrubland Alliance											
Arrow-weed Seasonally Flooded	LwFlt/ArdLw	0.0752	0.0821	0.0137	-0.0194	-0.0465	-0.0718	-0.0485	-0.0096	-0.0181	0.0424
Big Sagebrush Shrubland Alliance											
Big Sagebrush - (Rubber Rabbitbrush) / Cheatgrass Semi-natural	ArdLw	0.0364	0.0781	0.0419	0.0151	-0.0469	-0.0660	-0.0445	-0.0430	-0.0477	-0.0074
Big Sagebrush / Blue Grama	UpSnd	-0.0199	-0.0280	0.0227	0.0956	-0.0022	-0.0099	0.0041	0.0164	-0.0227	-0.0190
Basin Big Sagebrush Shrubland Alliance											
Basin Big Sagebrush / Western Wheatgrass - (Str. Wild Rye)	MsaTp	0.0223	-0.0711	-0.0104	-0.0127	-0.0312	0.0902	0.0811	0.0420	-0.0170	-0.0268
Mountain Big Sagebrush Shrubland Alliance											
Mountain Big Sagebrush / Needle-and-Thread	MsaTp/RckSl	0.0025	-0.0072	0.0392	0.0313	-0.0221	0.0264	0.0523	0.0116	-0.0272	-0.0307
(Stansbury Cliff-rose, Mexican Cliff-rose) Shrubland Alliance											
Stansbury Cliff-rose - Greenleaf Manzanita	UpSnd/RckSl	-0.0464	-0.0157	0.0903	0.0913	0.0418	0.0244	0.0246	-0.0432	-0.0422	-0.0622
Rubber Rabbitbrush Shrubland Alliance											
Rubber Rabbitbrush / Cheatgrass Semi-natural	RckSl/UpSnd	0.0036	0.0489	0.0925	0.0697	-0.0269	-0.0668	-0.0495	-0.0707	-0.0537	-0.0201

	Cluster[1]	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
III. SHRUBLAND (cont.)											
<u>Sand Sagebrush Shrubland Alliance</u>											
Sand Sagebrush Colorado Plateau	ArdLw	0.0276	0.0861	0.0369	0.0103	-0.0316	-0.0690	-0.0525	-0.0511	-0.0421	-0.0004
<u>Nevada Joint-fir Shrubland Alliance</u>											
Nevada Joint-fir Basalt	LwFlt/ArdLw	0.0961	0.1486	0.0207	-0.0204	-0.0509	-0.0852	-0.0684	-0.0517	-0.0405	-0.0139
<u>Mormon-tea Shrubland Alliance</u>											
Gray Horsebrush - Mormon-tea	UpSnd	-0.0231	0.0029	0.0589	0.0993	0.0032	-0.0324	-0.0125	-0.0380	-0.0328	-0.0212
<u>Blackbrush Shrubland Alliance</u>											
Blackbrush / James' Galleta	ArdLw	0.0477	0.2037	0.0586	-0.0488	-0.0706	-0.0861	-0.0701	-0.0675	-0.0653	-0.0432
Blackbrush	ArdLw	0.0591	0.1692	0.0466	-0.0290	-0.0600	-0.0745	-0.0595	-0.0695	-0.0605	-0.0327
<u>Fourwing Saltbush Shrubland Alliance</u>											
Fourwing Saltbush - Big Sagebrush	LwFlt/ArdLw	0.0954	0.1107	0.0064	-0.0267	-0.0576	-0.0758	-0.0631	-0.0460	-0.0461	-0.0115
Fourwing Saltbush	LwFlt/ArdLw	0.0864	0.1379	0.0241	-0.0258	-0.0509	-0.0783	-0.0648	-0.0620	-0.0524	-0.0251
<u>Mountain Snowberry Shrubland Alliance</u>											
Mountain Snowberry / Kentucky Bluegrass Semi-natural	HPltu	0.0232	-0.0419	-0.0253	0.0102	-0.0092	0.0036	0.0253	0.1238	0.0096	0.0214
<u>Utah Serviceberry Shrubland Alliance</u>											
Utah Serviceberry Shrubland	HPltu	-0.0105	-0.0158	0.0184	-0.0081	-0.0245	0.0201	0.0253	0.0651	0.0168	0.0181
<u>Gambel Oak Shrubland Alliance</u>											
Gambel Oak - Mountain-mahogany / (Geyer's Sedge)	MsaTp/RckSl	-0.0360	-0.0304	0.0604	0.0140	-0.0058	0.0699	0.0632	0.0114	-0.0143	-0.0427
Gambel Oak / Big Sagebrush	UpSnd/RckSl	-0.0139	-0.0193	0.0503	0.0458	-0.0108	0.0085	0.0166	0.0083	-0.0183	-0.0196
Gambel Oak / Mountain Snowberry	HPltu	-0.0133	-0.0650	-0.0049	0.0096	-0.0003	0.0521	0.0683	0.1088	0.0207	0.0038
Gambel Oak / Muttongrass	UpSnd/RckSl	-0.0330	-0.0376	0.0558	0.0686	0.0304	0.0241	0.0486	0.0113	-0.0024	-0.0228
Gambel Oak / Utah Serviceberry	MsaTp/RckSl	-0.0297	-0.0211	0.0641	0.0343	-0.0032	0.0363	0.0460	0.0101	-0.0178	-0.0286
<u>Water Birch Temporarily Flooded Shrubland Alliance</u>											
Fremont Cottonwood / Water Birch Wooded	Strmb/HPltu	-0.0225	-0.0277	-0.0108	-0.0128	0.0009	-0.0014	0.0005	0.0448	0.0421	0.1064
<u>Strapleaf Willow Temporarily Flooded Shrubland Alliance</u>											
Strapleaf Willow / Beaked Sedge	Strmb/HPltu	-0.0110	-0.0392	-0.0578	-0.0118	-0.0030	-0.0084	-0.0126	0.1070	0.0733	0.1149
<u>(Coyote Willow, Sandbar Willow) Temporarily Flooded Shrubland Alliance</u>											
Coyote Willow / Barren	--	0.0100	0.0450	0.0273	0.0545	-0.0368	-0.0746	-0.0713	-0.0464	-0.0204	0.0710
Coyote Willow / Mesic Graminoids	Strmb	-0.0075	-0.0222	-0.0435	-0.0036	-0.0087	-0.0315	-0.0250	0.0180	0.0475	0.2544

	Cluster[1]	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
IV. DWARF-SHRUBLAND											
Black Sagebrush Dwarf-shrubland Alliance											
Black Sagebrush / Bottlebrush	--	0.0176	0.0195	0.0215	0.0238	0.0094	-0.0173	0.0052	-0.0082	-0.0248	-0.0219
Black Sagebrush / Muttongrass	MsaTp/RckSl	-0.0180	-0.0101	0.0468	0.0361	0.0215	0.0340	0.0580	-0.0037	-0.0318	-0.0450
Black Sagebrush / Needle-and-Thread	UpSnd/RckSl	-0.0031	0.0230	0.0704	0.0474	-0.0041	-0.0101	0.0143	-0.0194	-0.0382	-0.0356
Snakeweed Dwarf-shrubland Alliance											
Snakeweed - (Prickly-pear species) / James' Galleta	ArdLw	0.0557	0.1171	0.0503	-0.0068	-0.0471	-0.0661	-0.0451	-0.0542	-0.0540	-0.0204
V. HERBACEOUS VEGETATION											
Intermediate Wheatgrass Semi-natural Herbaceous Alliance											
Intermediate Wheatgrass Semi-natural	HPltu	-0.0087	-0.0432	-0.0174	-0.0190	-0.0147	0.0089	0.0349	0.1599	0.0408	0.0487
Mountain Muhly Herbaceous Alliance											
(Sandhill Muhly, Mountain Muhly) - Hairy Goldenaster	Slrck/UpSnd	-0.0305	-0.0153	0.0481	0.1097	0.0557	-0.0134	-0.0024	-0.0167	-0.0156	-0.0148
Needle-and-Thread Bunch Herbaceous Alliance											
Needle-and-Thread Great Basin	--	0.0212	-0.0171	0.0041	0.0385	-0.0086	0.0052	0.0350	0.0378	-0.0027	-0.0083
Smooth Brome Semi-natural Herbaceous Alliance											
Smooth Brome - (Western Wheatgrass) Semi-natural	--	0.0931	-0.0306	-0.0070	-0.0175	-0.0124	0.0173	0.0624	0.0717	0.0021	0.0174
Sand Dropseed Herbaceous Alliance											
Sand Dropseed Great Basin	LwFlt/ArdLw	0.0686	0.0819	0.0181	0.0175	-0.0301	-0.0995	-0.0820	-0.0563	-0.0374	0.0469
James' Galleta Herbaceous Alliance											
James' Galleta	LwFlt/ArdLw	0.0877	0.1470	0.0421	-0.0409	-0.0600	-0.1016	-0.0797	-0.0669	-0.0596	-0.0165
Blue Grama Herbaceous Alliance											
Blue Grama - Needle-and-Thread	UpSnd	-0.0229	-0.0197	0.0485	0.0965	0.0109	-0.0001	0.0182	-0.0117	-0.0223	-0.0308
Baltic Rush Seasonally Flooded Herbaceous Alliance											
Baltic Rush	Strmb/HPltu	0.0144	-0.0256	-0.0491	-0.0162	-0.0073	-0.0267	-0.0133	0.0801	0.0315	0.1540
Kentucky Bluegrass Semi-natural Seasonally Flooded Herbaceous Alliance											
Kentucky Bluegrass Semi-natural Seasonally Flooded	--	0.0581	-0.0225	-0.0411	-0.0045	-0.0025	-0.0113	0.0234	0.1086	0.0064	0.0341
(Swollen-beak Sedge, Beaked Sedge) Seasonally Flooded Herbaceous Alliance											
Beaked Sedge	Strmb/HPltu	-0.0211	-0.0347	-0.0341	0.0063	0.0144	-0.0080	-0.0145	0.0198	0.0569	0.1332

	Cluster[1]	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
V. HERBACEOUS VEGETATION (cont.)											
Nebraska Sedge Seasonally Flooded Herbaceous Alliance											
Nebraska Sedge	Strmb/HPltu	-0.0169	-0.0402	-0.0439	0.0096	0.0197	-0.0189	-0.0137	0.0671	0.0526	0.1606
Green Rabbitbrush Shrub Herbaceous Alliance											
Green Rabbitbrush / Kentucky Bluegrass Semi-natural	--	0.0508	0.0253	-0.0073	0.0057	-0.0382	-0.0465	-0.0258	0.0349	-0.0229	0.0275
(Field Horsetail, Variegated Scouringrush) Semipermanently Flooded Herbaceous Alliance											
(Field Horsetail, Variegated Scouringrush)	Strmb	-0.0020	-0.0023	-0.0227	0.0133	-0.0139	-0.0569	-0.0468	0.0297	0.0219	0.2354
VII. SPARSE VEGETATION											
Wooded Bedrock Sparsely Vegetated Alliance											
Ponderosa Pine Slickrock	UpSnd/RckSl	-0.0389	-0.0118	0.0941	0.0791	0.0381	0.0123	0.0204	-0.0354	-0.0271	-0.0409
Littleleaf Mountain-mahogany Sparsely Vegetated Alliance											
Littleleaf Mountain-mahogany Slickrock	Slrck/UpSnd	-0.0428	-0.0225	0.0572	0.0899	0.1010	-0.0043	-0.0008	-0.0417	-0.0082	-0.0362
Mountain-mahogany Sparsely Vegetated Alliance											
Mountain-mahogany Rock Pavement	MsaTp/RckSl	-0.0364	-0.0268	0.0768	0.0301	-0.0053	0.0845	0.0628	-0.0280	-0.0347	-0.0565
Painted Desert Sparsely Vegetated Alliance											
Crispleaf Wild Buckwheat Badlands	ArdLw	0.0203	0.1338	0.0527	-0.0180	-0.0422	-0.0599	-0.0491	-0.0555	-0.0478	-0.0289
Nevada Joint-fir / Lichen	LwFlt/ArdLw	0.1295	0.1541	-0.0038	-0.0627	-0.0608	-0.0967	-0.0827	-0.0556	-0.0430	-0.0127
Xx. HIERARCHY PLACEMENT UNDETERMINED											
Emory Seepwillow Shrubland [Provisional]											
Emory Seepwillow	Strmb	-0.0004	-0.0124	-0.0214	-0.0201	-0.0025	-0.0408	-0.0396	0.0225	0.0431	0.2246
Rubber Rabbitbrush Sand Deposit Sparse Vegetation [Provisional]											
Rubber Rabbitbrush Sand Deposit	RckSl/UpSnd	0.0115	0.0194	0.0318	0.0634	0.0060	-0.0492	-0.0413	-0.0293	-0.0184	0.0072

[1] Clusters identifed through hierarchial clustering of NVCS associations using coalition group affinities shown here (see Fig. 2.15).

ArdLw = Arid Lowlands Woodland/Shrub/Sparse; **CrvcC** = Crevice Canyon Forest/Woodland; **CrvcC/HPltu** = Crevice Canyon/High Plateau Forest/Woodland
HPltu = High Plateau Forest/Shrub/Herb; **LwFlt/ArdLw** = Lowland Flats/Arid Lowlands Shrub/Herb/Sparse
MsaTp = Mesa Top Forest/Woodland/Shrub; **MsaTp/RckSl** = Mesa Top/Rocky Slopes Woodland/Shrub/Sparse
RckSl = Rocky Slopes Woodland/Shrub; **RckSl/UpSnd** = Rocky Slopes/Upland Sands Shrub/Sparse; **Slrck/UpSnd** = Slickrock/Upland Sands Herb/Sparse
Strmb = Streambank Forest/Woodland/ Shrub/Herb; **Strmb/HPltu** = Streambank/High Plateau Woodland/Shrub/Herb
UpSnd = Upland Sands Shrub/Herb; **UpSnd/RckSl** = Upland Sands/Rocky Slopes Woodland/Shrub/Sparse

APPENDIX 2.5

Vegetation map units of Zion National Park, Utah as mapped by Cogan et al. (2004) (rows) with their spatial correspondence to coalition species groups of the current study (columns). Regression tree modeling of was used to create predictive maps of plot-averaged species group affinities (in units of the phi coefficient) across the entire park at a 10 m pixel resolution, and these affinity values were then averaged within vegetation map units to give the values shown here. Low values (green shading) indicate low correspondence between map units and coalition groups; high values (red shading) indicate high correspondence (shading is scaled separately for each column). Map units are grouped into eight higher units following USGS (2004).

	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Bare - Soil/Stone Formations										
Basalt Talus	-0.0091	-0.0026	0.0360	0.0121	-0.0071	0.0136	0.0242	0.0738	0.0044	-0.0186
Carmel Formation (Limestone)	-0.0367	-0.0392	0.0009	0.0200	0.0076	0.0976	0.0868	0.1121	0.0334	0.0005
Chinle Formation - Petrified Forest (Shale)	0.0098	0.1266	0.0667	-0.0098	-0.0249	-0.0518	-0.0419	-0.0386	-0.0286	-0.0290
Chinle Formation - Shinarump (Shale)	0.0078	0.1070	0.0704	-0.0014	-0.0167	-0.0289	-0.0330	-0.0361	-0.0270	-0.0334
Gullies and Eroded Lands	-0.0055	0.0579	0.0629	0.0089	-0.0119	-0.0272	-0.0230	-0.0258	-0.0128	-0.0045
Kaibab Formation (Limestone)	-0.0368	-0.0142	0.0692	0.0187	-0.0260	-0.0053	-0.0091	-0.0399	-0.0298	-0.0349
Kayenta Formation (Sandstone)	-0.0029	0.0989	0.0880	0.0061	-0.0192	-0.0394	-0.0336	-0.0328	-0.0205	-0.0290
Moenave Formation (Sandstone)	-0.0103	0.1133	0.0735	0.0006	-0.0235	-0.0321	-0.0347	-0.0340	-0.0214	-0.0310
Moenkopi Formation (Conglomerate)	0.0127	0.0829	0.0689	-0.0010	-0.0252	-0.0306	-0.0211	-0.0364	-0.0248	-0.0322
Navajo Formation (Sandstone)	-0.0363	-0.0216	0.0631	0.0789	0.0749	0.0161	0.0069	-0.0126	0.0034	-0.0273
Slides (Fans and Slumps)	-0.0060	0.0883	0.0733	0.0044	-0.0166	-0.0365	-0.0306	-0.0317	-0.0176	-0.0270
Temple Cap (Sandstone)	-0.0363	-0.0378	-0.0060	0.0220	0.0055	0.0929	0.0842	0.1023	0.0346	0.0023
Unvegetated Volcanic Cinders and Cinder Cones	-0.0095	0.1324	0.0692	-0.0118	-0.0260	-0.0598	-0.0426	-0.0383	-0.0298	-0.0349
Volcanic and Basalt Cliffs	-0.0023	0.1191	0.0691	-0.0049	-0.0228	-0.0248	-0.0369	-0.0377	-0.0283	-0.0346
Grasslands										
Cheatgrass Annual Disturbed Grassland	0.0189	0.0177	0.0220	0.0198	-0.0165	-0.0085	-0.0059	-0.0205	-0.0191	0.0098
Dry Meadow Mixed Herbaceous Vegetation Mosaic	-0.0140	-0.0319	0.0363	0.0260	-0.0119	0.0298	0.0414	0.0323	-0.0005	-0.0195
James' Galleta Herbaceous Vegetation	0.0470	0.0938	0.0451	-0.0108	-0.0253	-0.0593	-0.0424	-0.0399	-0.0298	-0.0104
Mountain Snowberry / Kentucky Bluegrass Semi-natural Shrb.	-0.0237	-0.0381	0.0022	0.0285	-0.0134	0.0359	0.0453	0.0879	0.0287	-0.0067
Perennial Disturbed Grassland Complex	-0.0111	-0.0297	0.0315	0.0332	-0.0059	0.0304	0.0355	0.0392	-0.0012	-0.0174
Sand Dropseed Great Basin Herbaceous Vegetation	0.0431	0.0628	0.0104	-0.0061	-0.0229	-0.0514	-0.0370	-0.0390	-0.0283	0.0474

	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Higher Elevation Forest										
Douglas-fir Forest Alliance	-0.0330	-0.0271	0.0436	0.0463	0.0615	0.0188	0.0106	-0.0013	0.0515	-0.0101
Ponderosa Pine / Gambel Oak Woodland Complex	-0.0295	-0.0287	0.0485	0.0433	0.0282	0.0345	0.0340	0.0062	0.0058	-0.0252
Ponderosa Pine / Greenleaf Manzanita Woodland	-0.0348	-0.0188	0.0611	0.0724	0.0592	0.0228	0.0175	-0.0121	-0.0083	-0.0315
Ponderosa Pine / Mixed Herbaceous Woodland Complex	-0.0250	-0.0332	0.0318	0.0274	-0.0104	0.0313	0.0419	0.0410	0.0054	-0.0185
Ponderosa Pine Forest (Closed Canopy)	-0.0268	-0.0392	0.0405	0.0315	0.0032	0.0626	0.0585	0.0068	-0.0043	-0.0332
Quaking Aspen Forest Complex	-0.0232	-0.0392	-0.0099	0.0187	-0.0127	0.0327	0.0474	0.1196	0.0363	0.0030
Snags	-0.0205	-0.0392	0.0271	0.0234	-0.0048	0.0441	0.0499	0.0519	0.0097	-0.0174
White Fir Forest Alliance	-0.0289	-0.0347	0.0202	0.0327	0.0223	0.0490	0.0484	0.0730	0.0274	-0.0076
Higher Elevation Shrub										
Bigtooth Maple / Gambel Oak Forest	-0.0226	-0.0389	0.0051	0.0257	0.0063	0.0475	0.0543	0.0868	0.0277	-0.0051
Black Sagebrush Dwarf-shrubland Complex	-0.0211	-0.0387	0.0107	0.0204	-0.0178	0.0299	0.0447	0.0977	0.0211	-0.0092
Gambel Oak Shrubland Alliance	-0.0274	-0.0278	0.0446	0.0291	0.0079	0.0471	0.0480	0.0123	-0.0003	-0.0276
Gambel Oak Woodland	-0.0214	-0.0266	0.0416	0.0318	0.0052	0.0353	0.0382	0.0156	0.0011	-0.0248
Greenleaf Manzanita - Gambel Oak - (Utah Serviceberry) Shrb.	-0.0306	-0.0350	0.0457	0.0455	0.0234	0.0496	0.0466	0.0282	0.0029	-0.0255
Greenleaf Manzanita Shrubland Complex	-0.0332	-0.0077	0.0589	0.0630	0.0440	0.0168	0.0160	-0.0113	-0.0096	-0.0306
Mixed Mountain Shrubland Complex	-0.0319	-0.0309	0.0517	0.0344	0.0140	0.0544	0.0534	0.0077	-0.0046	-0.0307
Mountain-mahogany Rock Pavement Sparse Vegetation	-0.0367	-0.0392	0.0185	0.0200	0.0072	0.0993	0.0883	0.0685	0.0136	-0.0168
Utah Serviceberry Shrubland	-0.0322	-0.0362	0.0487	0.0233	-0.0067	0.0479	0.0551	0.0154	-0.0014	-0.0289
Lower Elevation Forest (Pinyon/Juniper)										
Juniper / Big Sagebrush Woodland Complex	0.0065	0.1108	0.0619	-0.0034	-0.0210	-0.0454	-0.0365	-0.0387	-0.0283	-0.0240
Pinyon - Juniper / Gamble Oak Woodland Complex	-0.0243	-0.0112	0.0567	0.0292	0.0028	0.0308	0.0335	-0.0093	-0.0118	-0.0316
Pinyon - Juniper Woodland Complex	-0.0136	0.0483	0.0683	0.0196	-0.0047	-0.0128	-0.0071	-0.0292	-0.0213	-0.0296
Lower Elevation Shrub										
Big Sagebrush Shrubland Complex	-0.0008	0.0245	0.0425	0.0284	-0.0166	-0.0071	0.0005	-0.0202	-0.0193	-0.0235
Blackbrush Shrubland Complex	0.0418	0.1012	0.0300	-0.0088	-0.0223	-0.0564	-0.0425	-0.0397	-0.0297	0.0001
Croplands and Pastures	-0.0001	0.0024	0.0355	0.0501	-0.0254	0.0034	0.0039	-0.0267	-0.0212	-0.0336
Mixed Urban or Built-up Land	0.0625	0.0621	-0.0088	-0.0084	-0.0256	-0.0541	-0.0381	-0.0364	-0.0288	0.0501
Nevada Joint-fir Basalt Shrubland	0.0110	0.1035	0.0607	-0.0082	-0.0143	-0.0409	-0.0420	-0.0386	-0.0283	-0.0197
Other Agricultural Lands	-0.0249	-0.0392	0.0346	0.0187	-0.0114	0.0621	0.0656	0.1219	-0.0056	-0.0140

	Lowland Flats	Arid Lowlands	Rocky Slopes	Upland Sands	Slickrock	Xeric Mesa Top	Mesic Mesa Top	High Plateau	Crevice Canyon	Stream-bank
Lower Elevation Shrub (cont.)										
Painted Desert Sparsely Vegetated Alliance	0.0553	0.1308	0.0679	-0.0117	-0.0259	-0.0575	-0.0425	-0.0395	-0.0295	-0.0320
Rabbitbrush Shrubland Complex	0.0144	0.0303	0.0243	0.0061	-0.0116	-0.0170	-0.0082	-0.0118	-0.0116	0.0173
Sand Sagebrush Colorado Plateau Shrubland	0.0077	0.0679	0.0394	0.0048	-0.0082	-0.0429	-0.0351	-0.0382	-0.0276	0.0033
Snakeweed -(Prickly-pear) / James' Galleta Dwarf-shrubland	0.0159	0.0930	0.0503	-0.0006	-0.0137	-0.0441	-0.0343	-0.0338	-0.0245	-0.0140
Strip Mines, Quarries, and Gravel Pits	-0.0120	0.0311	0.0400	0.0187	-0.0260	-0.0275	-0.0091	-0.0399	-0.0298	-0.0126
Talus Mixed Shrubland	-0.0186	0.0387	0.0698	0.0306	0.0155	-0.0135	-0.0141	-0.0264	-0.0094	-0.0260
Transportation, Communications, and Utilities	-0.0011	0.0260	0.0403	0.0180	-0.0115	-0.0095	-0.0010	-0.0163	-0.0182	-0.0055
Riparian/Flooded Woodland										
Boxelder Woodland Alliance	-0.0180	0.0101	0.0477	0.0300	0.0129	-0.0136	-0.0113	-0.0212	0.0097	-0.0118
Cattail, Bulrush, Emergent Wetland Complex	-0.0133	-0.0064	0.0710	0.0187	-0.0260	0.0027	0.0199	0.0464	-0.0169	-0.0208
Emory Seepwillow Shrubland	0.0242	0.0620	-0.0026	-0.0095	-0.0220	-0.0476	-0.0413	-0.0351	-0.0198	0.1421
Fremont Cottonwood - Velvet Ash Woodland	0.0011	0.0344	0.0519	0.0103	0.0062	-0.0198	-0.0257	-0.0198	0.0034	0.0068
Fremont Cottonwood Woodland Complex	0.0297	0.0585	0.0150	-0.0055	-0.0190	-0.0452	-0.0375	-0.0331	-0.0179	0.0669
Intermittent Streams	-0.0151	0.0257	0.0491	0.0259	0.0056	-0.0158	-0.0088	-0.0150	0.0022	0.0028
Perennial Streams	-0.0011	0.0407	0.0229	0.0052	-0.0134	-0.0343	-0.0297	-0.0192	0.0105	0.0586
Reservoirs	-0.0011	-0.0392	-0.0071	0.0206	0.0056	0.0300	0.0373	0.0880	0.0664	-0.0030
Russian Olive Semi-natural Woodland	0.0499	0.0651	-0.0151	-0.0118	-0.0260	-0.0510	-0.0426	-0.0399	-0.0298	0.1060
Sand Bars and Beaches	0.0066	0.0467	0.0220	0.0084	-0.0248	-0.0347	-0.0225	-0.0364	-0.0247	0.0440
Sandbar Willow Shrubland Alliance	-0.0063	0.0429	0.0343	0.0159	-0.0119	-0.0292	-0.0187	-0.0305	-0.0151	0.0183
Sedge-Rush Wet Meadow Herbaceous Vegetation Mosaic	-0.0097	-0.0366	0.0003	0.0196	-0.0168	0.0376	0.0491	0.0880	0.0263	-0.0048
Stock Ponds	-0.0044	-0.0392	0.0177	0.0302	-0.0046	0.0304	0.0407	0.0636	0.0141	-0.0088
Strapleaf Willow / Beaked Sedge Shrubland	-0.0225	-0.0368	0.0068	0.0290	0.0061	0.0268	0.0324	0.0684	0.0428	-0.0080
Tamarisk spp. Temporarily Flooded Shrubland	0.0144	0.0823	0.0050	-0.0118	-0.0260	-0.0481	-0.0426	-0.0399	-0.0298	0.1326
Tinajas (natural water holes / tanks)	-0.0368	0.0228	0.0692	0.0562	0.0491	-0.0178	-0.0066	-0.0246	-0.0074	-0.0243
Slickrock										
Littleleaf Mountain-mahogany Slickrock Sparse Vegetation	-0.0364	-0.0007	0.0668	0.0787	0.0640	0.0026	0.0018	-0.0225	-0.0138	-0.0317
Ponderosa Pine Slickrock Sparse Vegetation	-0.0363	-0.0124	0.0669	0.0836	0.0716	0.0103	0.0048	-0.0180	-0.0109	-0.0317

APPENDIX 3.1

Vascular plant genera and species included in niche overlap analyses for plant communities of Zion National Park, Utah, showing correspondence between different taxonomic concepts. Genus names follow NCBI (2008), species names follow Welsh et al. (2003) and database names follow Kartesz (1999). #In=number of plot records (out of 332) in the 1999-2000 USGS-NPS Zion N.P. vegetation survey database in which the taxon was recorded within the plot (i.e., cover>0); #Out=number of additional plot records in which the taxon was recorded near but not within the plot (i.e., cover=0). All records (#In + #Out) where used in presence-based niche overlap analyses, but only within-plot records were used in cover-based analyses.

Genus	Species	Database Name	#In	#Out
Abies	*Abies concolor*	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.	33	5
Abronia	*Abronia fragrans*	*Abronia fragrans* Nutt. ex Hook.	4	
Acer	*Acer grandidentatum*	*Acer grandidentatum* Nutt.	32	3
Acer	*Acer negundo*	*Acer negundo* L.	23	2
Achillea	*Achillea millefolium*	*Achillea millefolium* L.	24	
Achnatherum	*Stipa hymenoides*	*Achnatherum contractum* (B.L. Johnson) Barkworth	1	
Achnatherum	*Stipa hymenoides*	*Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth	54	4
Achnatherum	*Stipa lettermanii*	*Achnatherum lettermanii* (Vasey) Barkworth	12	
Achnatherum	*Stipa nelsonii*	*Achnatherum nelsonii* ssp. *nelsonii* (Scribn.) Barkworth	2	
Achnatherum	*Stipa speciosa*	*Achnatherum speciosum* (Trin. & Rupr.) Barkworth	5	
Agastache	*Agastache urticifolia*	*Agastache urticifolia* (Benth.) Kuntze	3	
Agoseris		*Agoseris* Raf.	2	1
Agropyron	*Agropyron cristatum*	*Agropyron cristatum* (L.) Gaertn.	3	
Agrostis	*Agrostis exarata*	*Agrostis exarata* Trin.	3	
Agrostis	*Agrostis stolonifera*	*Agrostis stolonifera* L.	4	
Agrostis		*Agrostis* L.	2	
Allionia	*Allionia incarnata*	*Allionia incarnata* L.	1	
Allium		*Allium* L.	6	1
Ambrosia	*Ambrosia acanthicarpa*	*Ambrosia acanthicarpa* Hook.	1	
Amelanchier	*Amelanchier alnifolia*	*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roemer	17	
Amelanchier	*Amelanchier utahensis*	*Amelanchier utahensis* Koehne	136	2
Andropogon	*Andropogon gerardii*	*Andropogon gerardii* Vitman	1	
Antennaria	*Antennaria dimorpha*	*Antennaria dimorpha* (Nutt.) Torr. & Gray	4	
Antennaria		*Antennaria* Gaertn.	7	
Apocynum	*Apocynum androsaemifolium*	*Apocynum androsaemifolium* L.	1	
Aquilegia		*Aquilegia* L.	1	1
Arabis	*Arabis holboellii*	*Arabis holboellii* Hornem.	8	
Arabis	*Arabis perennans*	*Arabis perennans* S. Wats.	1	
Arabis		*Arabis* L.	19	
Arctostaphylos	*Arctostaphylos patula*	*Arctostaphylos patula* Greene	89	2
Arctostaphylos	*Arctostaphylos pungens*	*Arctostaphylos pungens* Kunth	11	
Arenaria	*Arenaria fendleri*	*Arenaria fendleri* Gray	25	
Arenaria	*Arenaria macradenia*	*Arenaria macradenia* S. Wats.	14	
Arenaria		*Arenaria* L.	3	

Genus	Species	Database Name	#In	#Out
Aristida	*Aristida purpurascens*	*Aristida purpurascens* Poir.	2	
Aristida	*Aristida purpurea*	*Aristida purpurea* Nutt.	18	
Arnica		*Arnica* L.	1	
Artemisia	*Artemisia campestris*	*Artemisia campestris* L.	13	
Artemisia	*Artemisia dracunculus*	*Artemisia dracunculus* L.	10	
Artemisia	*Artemisia dracunculus*	*Artemisia dracunculus* ssp. *dracunculus* L.	1	
Artemisia	*Artemisia filifolia*	*Artemisia filifolia* Torr.	10	
Artemisia	*Artemisia ludoviciana*	*Artemisia ludoviciana* Nutt.	47	1
Artemisia	*Artemisia nova*	*Artemisia nova* A. Nels.	22	1
Artemisia	*Artemisia tridentata*	*Artemisia tridentata* Nutt.	63	
Artemisia	*Artemisia tridentata*	*Artemisia tridentata* ssp. *tridentata* Nutt.	2	
Artemisia	*Artemisia tridentata*	*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle	9	
Asclepias	*Asclepias subverticillata*	*Asclepias subverticillata* (Gray) Vail	2	
Asclepias		unknown milkweed	1	
Asplenium		*Asplenium* L.	1	
Asteraceae spp.		Asteraceae	1	
Asteraceae spp.		unknown aster	1	
Asteraceae spp.		unknown aster 2	1	
Asteraceae spp.		unknown composite	4	
Asteraceae spp.		unknown forb composite	1	
Asterinae spp.		*Aster* L.	8	
Astragalus	*Astragalus flavus*	*Astragalus flavus* Nutt.	2	
Astragalus	*Astragalus subcinereus*	*Astragalus subcinereus* Gray	2	
Astragalus		*Astragalus* L.	30	1
Atriplex	*Atriplex canescens*	*Atriplex canescens* (Pursh) Nutt.	12	
Atriplex		*Atriplex confertifolia* (Torr. & Frem.) S. Wats.	2	
Atriplex		*Atriplex* L.	1	
Baccharis	*Baccharis salicina*	*Baccharis emoryi* Gray	9	
Baccharis	*Baccharis salicina*	*Baccharis salicifolia* (Ruiz & Pavon) Pers.	4	
Baccharis		*Baccharis* L.	1	
Baileya	*Baileya multiradiata*	*Baileya multiradiata* Harvey & Gray ex Gray	1	
Balsamorhiza	*Balsamorhiza sagittata*	*Balsamorhiza sagittata* (Pursh) Nutt.	9	1
Betula	*Betula occidentalis*	*Betula occidentalis* Hook.	6	1
Boraginaceae spp.		unknown borage	1	
Boraginaceae spp.		unknown forb - borage	1	
Bouteloua	*Bouteloua barbata*	*Bouteloua barbata* Lag.	1	
Bouteloua	*Bouteloua gracilis*	*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths	31	1
Brassicaceae spp.		*Brassica* L.	1	
Brassicaceae spp.		brassicaceae unknown	1	
Brassicaceae spp.		mustard	4	
Brassicaceae spp.		Mustard - small	1	
Brassicaceae spp.		mustard species	5	
Brassicaceae spp.		unknown mustard	2	
Brickellia	*Brickellia atractyloides*	*Brickellia atractyloides* Gray	3	
Brickellia	*Brickellia californica*	*Brickellia californica* (Torr. & Gray) Gray	3	
Brickellia	*Brickellia grandiflora*	*Brickellia grandiflora* (Hook.) Nutt.	5	
Brickellia	*Brickellia longifolia*	*Brickellia longifolia* S. Wats.	6	

Genus	Species	Database Name	#In	#Out
Brickellia	*Brickellia microphylla*	*Brickellia microphylla* (Nutt.) Gray	1	1
Brickellia		*Brickellia* Ell.	7	1
Bromus	*Bromus anomalus*	*Bromus anomalus* Rupr. ex Fourn.	7	
Bromus	*Bromus diandrus*	*Bromus diandrus* Roth	15	
Bromus	*Bromus inermis*	*Bromus inermis* Leyss.	12	1
Bromus	*Bromus rubens*	*Bromus rubens* L.	6	
Bromus	*Bromus tectorum*	*Bromus tectorum* L.	93	1
Bromus		*Bromus* L.	3	
Calamagrostis		*Calamagrostis* Adans.	1	
Calochortus	*Calochortus nuttallii*	*Calochortus nuttallii* Torr. & Gray	6	1
Calochortus		*Calochortus* Pursh	3	
Carex	*Carex geyeri*	*Carex geyeri* Boott	2	
Carex	*Carex microptera*	*Carex microptera* Mackenzie	5	
Carex	*Carex nebrascensis*	*Carex nebrascensis* Dewey	2	
Carex	*Carex occidentalis*	*Carex occidentalis* Bailey	8	
Carex	*Carex rossii*	*Carex rossii* Boott	10	
Carex	*Carex utriculata*	*Carex utriculata* Boott	2	
Carex		*Carex* L.	18	1
Carex		*Carex* L. (*occidentalis*?)	1	
Carex		*Carex* L. (*rossii*?)	1	
Caryophyllaceae spp.		unknown caryophyllaceae	2	
Castilleja	*Castilleja chromosa*	*Castilleja applegatei* ssp. *martinii* (Abrams) Chuang & Heckard	3	
Castilleja	*Castilleja flava*	*Castilleja flava* var. *flava* S. Wats.	1	
Castilleja	*Castilleja linariifolia*	*Castilleja linariifolia* Benth.	7	
Castilleja		*Castilleja* Mutis ex L. f.	6	
Ceanothus	*Ceanothus fendleri*	*Ceanothus fendleri* Gray	4	1
Ceanothus	*Ceanothus martinii*	*Ceanothus martinii* M.E. Jones	2	
Ceanothus		*Ceanothus* L.	1	
Celtis	*Celtis reticulata*	*Celtis laevigata* var. *reticulata* (Torr.) L. Benson	4	1
Cenchrus	*Cenchrus longispinus*	*Cenchrus longispinus* (Hack.) Fern.	1	
Cercocarpus	*Cercocarpus intricatus*	*Cercocarpus intricatus* S. Wats.	18	3
Cercocarpus	*Cercocarpus ledifolius*	*Cercocarpus ledifolius* Nutt.	2	
Cercocarpus	*Cercocarpus montanus*	*Cercocarpus montanus* Raf.	44	1
Chaenactis	*Chaenactis douglasii*	*Chaenactis douglasii* (Hook.) Hook. & Arn.	9	
Chaenactis	*Chaenactis stevioides*	*Chaenactis stevioides* Hook. & Arn.	1	
Chaenactis		*Chaenactis* DC.	2	
Chaenactis		*Chaenactis* DC. (*douglasii* or *stevioides*??)	1	
Chaetopappa	*Chaetopappa ericoides*	*Chaetopappa ericoides* (Torr.) Nesom	1	
Chamaesyce	*Chamaesyce albomarginata*	*Chamaesyce albomarginata* (Torr. & Gray) Small	1	
Chamaesyce	*Chamaesyce fendleri*	*Chamaesyce fendleri* (Torr. & Gray) Small	7	
Chamaesyce	*Chamaesyce glyptosperma*	*Chamaesyce glyptosperma* (Engelm.) Small	4	
Chamaesyce	*Chamaesyce parryi*	*Chamaesyce parryi* (Engelm.) Rydb.	1	
Chenopodium	*Chenopodium album*	*Chenopodium album* L.	2	
Chenopodium	*Chenopodium fremontii*	*Chenopodium fremontii* S. Wats.	4	
Chenopodium		*Chenopodium* L.	1	
Chimaphila	*Chimaphila umbellata*	*Chimaphila umbellata* (L.) W. Bart.	1	

Genus	Species	Database Name	#In	#Out
Chrysopsis	*Chrysopsis villosa*	*Heterotheca villosa* (Pursh) Shinners	59	
Chrysopsis	*Chrysopsis villosa*	*Heterotheca viscida* (Gray) Harms	1	
Chrysothamnus	*Chrysothamnus depressus*	*Chrysothamnus depressus* Nutt.	3	
Chrysothamnus	*Chrysothamnus viscidiflorus*	*Chrysothamnus viscidiflorus* (Hook.) Nutt.	12	
Chrysothamnus	*Chrysothamnus viscidiflorus*	*Chrysothamnus viscidiflorus* ssp. *axillaris* (Keck) L.C. Anders.	1	
Chrysothamnus		*Chrysothamnus* Nutt.	1	
Cirsium	*Cirsium arizonicum*	*Cirsium arizonicum* (Gray) Petrak	1	
Cirsium	*Cirsium calcareum*	*Cirsium calcareum* (M.E. Jones) Woot. & Standl.	1	
Cirsium	*Cirsium vulgare*	*Cirsium vulgare* (Savi) Ten.	1	
Cirsium	*Cirsium wheeleri*	*Cirsium wheeleri* (Gray) Petrak	6	
Cirsium		*Cirsium* P. Mill.	16	
Claytonia	*Montia perfoliata*	*Claytonia perfoliata* ssp. *perfoliata* var. *nubigena* (Greene) Poelln.	4	
Clematis	*Clematis columbiana*	*Clematis columbiana* (Nutt.) Torr. & Gray	2	
Clematis	*Clematis ligusticifolia*	*Clematis ligusticifolia* Nutt.	9	
Clematis		*Clematis* L.	1	
Coleogyne	*Coleogyne ramosissima*	*Coleogyne ramosissima* Torr.	12	
Collinsia	*Collinsia parviflora*	*Collinsia parviflora* Lindl.	1	
Comandra	*Comandra umbellata*	*Comandra umbellata* (L.) Nutt.	37	1
Comandra	*Comandra umbellata*	*Comandra umbellata* ssp. *pallida* (A. DC.) Piehl	2	
Convolvulus	*Convolvulus arvensis*	*Convolvulus arvensis* L.	2	
Cordylanthus	*Cordylanthus kingii*	*Cordylanthus kingii* S. Wats.	2	
Cordylanthus	*Cordylanthus parviflorus*	*Cordylanthus parviflorus* (Ferris) Wiggins	4	
Crepis	*Crepis intermedia*	*Crepis intermedia* Gray	1	
Cryptantha	*Cryptantha humilis*	*Cryptantha humilis* (Gray) Payson	2	
Cryptantha		*Cryptantha* Lehm. ex G. Don	14	
Cupressus	*Cupressus arizonica*	*Cupressus arizonica* Greene	1	
Dactylis	*Dactylis glomerata*	*Dactylis glomerata* L.	3	
Dalea	*Dalea searlsiae*	*Dalea searlsiae* (Gray) Barneby	3	
Datura	*Datura wrightii*	*Datura wrightii* Regel	5	
Datura		*Datura* L.	1	
Descurainia	*Descurainia pinnata*	*Descurainia pinnata* (Walt.) Britt.	1	
Descurainia		*Descurainia* Webb & Berth.	1	
Distichlis	*Distichlis spicata*	*Distichlis spicata* (L.) Greene	1	
Draba		*Draba* L.	4	
Dracocephalum	*Dracocephalum parviflorum*	*Dracocephalum parviflorum* Nutt.	1	
Echinocereus	*Echinocereus engelmannii*	*Echinocereus engelmannii* (Parry ex Engelm.) Lem.	8	1
Echinocereus	*Echinocereus triglochidiatus*	*Echinocereus triglochidiatus* Engelm.	10	1
Echinocereus		*Echinocereus* Engelm.	3	
Elaeagnus	*Elaeagnus angustifolia*	*Elaeagnus angustifolia* L.	2	2
Eleocharis		*Eleocharis* R. Br.	1	
Elymus	*Elymus canadensis*	*Elymus canadensis* L.	2	
Elymus	*Elymus elymoides*	*Elymus elymoides* (Raf.) Swezey	57	
Elymus	*Elymus elymoides*	*Elymus elymoides* ssp. *elymoides* (Raf.) Swezey	1	
Elymus	*Elymus glaucus*	*Elymus glaucus* Buckl.	1	
Elymus	*Elymus hispidus*	*Elytrigia intermedia* (Host) Nevski	2	
Elymus	*Elymus hispidus*	*Elytrigia intermedia* ssp. *intermedia* (Host) Nevski	1	
Elymus	*Elymus lanceolatus*	*Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould	11	

Genus	**Species**	**Database Name**	**#In**	**#Out**
Elymus	*Elymus repens*	*Elytrigia repens* (L.) Desv. ex B.D. Jackson	6	
Elymus	*Elymus smithii*	*Pascopyrum smithii* (Rydb.) A. Love	9	
Elymus	*Elymus spicatus*	*Pseudoroegneria spicata* ssp. *spicata* (Pursh) A. Love	1	
Elymus		*Elymus* L.	10	
Ephedra	*Ephedra nevadensis*	*Ephedra nevadensis*	1	
Ephedra	*Ephedra nevadensis*	*Ephedra nevadensis* S. Wats.	16	2
Ephedra	*Ephedra viridis*	*Ephedra viridis* Coville	20	5
Epilobium	*Epilobium brachycarpum*	*Epilobium brachycarpum* K. Presl	7	
Epilobium	*Zauschneria latifolia*	*Epilobium canum* ssp. *garrettii* (A. Nels.) Raven	1	
Epilobium	*Zauschneria latifolia*	*Epilobium canum* ssp. *latifolium* (Hook.) Raven	3	
Equisetum	*Equisetum arvense*	*Equisetum arvense* L.	5	
Equisetum	*Equisetum hyemale*	*Equisetum hyemale* L.	3	
Equisetum	*Equisetum laevigatum*	*Equisetum laevigatum* A. Braun	6	
Equisetum	*Equisetum variegatum*	*Equisetum variegatum* Schleich. ex F. Weber & D.M.H. Mohr	4	
Equisetum		*Equisetum* L.	2	1
Ericameria	*Chrysothamnus nauseosus*	*Ericameria nauseosa* ssp. *nauseosa* var. *nauseosa*	37	2
Ericameria	*Chrysothamnus parryi*	*Ericameria parryi* var. *parryi* (Gray) Nesom	1	
Ericameria	*Haplopappus linearifolius*	*Ericameria linearifolia* (DC.) Urbatsch & Wussow	4	
Erigeron	*Erigeron argentatus*	*Erigeron argentatus* Gray	1	
Erigeron	*Erigeron divergens*	*Erigeron divergens* Torr. & Gray	1	
Erigeron	*Erigeron pumilus*	*Erigeron concinnus* var. *concinnus* (Hook. & Arn.) Torr. & Gray	1	
Erigeron	*Erigeron pumilus*	*Erigeron pumilus* Nutt.	1	
Erigeron	*Erigeron speciosus*	*Erigeron speciosus* (Lindl.) DC.	2	
Erigeron	*Erigeron speciosus*	*Erigeron speciosus* var. *macranthus* (Nutt.) Cronq.	1	
Erigeron	*Erigeron utahensis*	*Erigeron utahensis* Gray	6	
Erigeron		*Erigeron* L.	34	1
Eriogonum	*Eriogonum corymbosum*	*Eriogonum corymbosum* Benth.	1	
Eriogonum	*Eriogonum fasciculatum*	*Eriogonum fasciculatum* Benth.	1	
Eriogonum	*Eriogonum flavum*	*Eriogonum flavum* Nutt.	1	
Eriogonum	*Eriogonum inflatum*	*Eriogonum inflatum* Torr. & Frem.	3	
Eriogonum	*Eriogonum microthecum*	*Eriogonum microthecum* Nutt.	4	1
Eriogonum	*Eriogonum ovalifolium*	*Eriogonum ovalifolium* Nutt.	1	
Eriogonum	*Eriogonum panguicense*	*Eriogonum panguicense* (M.E. Jones) Reveal	2	
Eriogonum	*Eriogonum racemosum*	*Eriogonum racemosum* Nutt.	20	
Eriogonum	*Eriogonum umbellatum*	*Eriogonum umbellatum* Torr.	24	
Eriogonum		*Eriogonum* Michx.	21	
Eriogonum		*Eriogonum*2 Michx.	2	
Erioneuron	*Erioneuron pulchellum*	*Erioneuron pulchellum* (Kunth) Tateoka	1	
Erodium	*Erodium cicutarium*	*Erodium cicutarium* (L.) L'Her. ex Ait.	6	
Erysimum	*Erysimum asperum*	*Erysimum capitatum* var. *argillosum* (Greene) R.J. Davis	7	
Erysimum	*Erysimum asperum*	*Erysimum capitatum* var. *capitatum* (Dougl. ex Hook.) Greene	1	
Euphorbia	*Euphorbia brachycera*	*Euphorbia brachycera* Engelm.	1	
Euphorbia		*Euphorbia* L.	14	
Eurybia	*Aster glaucodes*	*Aster glaucodes* Blake	1	
Fabaceae spp.		*Fabaceae* sp.	1	
Fabaceae spp.		legume species	1	
Fendlerella	*Fendlerella utahensis*	*Fendlerella utahensis* (S. Wats.) Heller	2	

Genus	Species	Database Name	#In	#Out
Festuca	*Festuca occidentalis*	*Festuca occidentalis* Hook.	1	
Festuca	*Festuca octoflora*	*Vulpia octoflora* var. *octoflora* (Walt.) Rydb.	4	
Festuca		*Festuca* L.	2	
Fraxinus	*Fraxinus anomala*	*Fraxinus anomala* Torr. ex S. Wats.	28	4
Fraxinus	*Fraxinus velutina*	*Fraxinus velutina* Torr.	6	
Gaillardia		*Gaillardia* Foug.	1	
Galium	*Galium aparine*	*Galium aparine* L.	1	
Galium		*Galium* L.	6	
Gayophytum		*Gayophytum* A. Juss.	1	
Geraea	*Geraea canescens*	*Geraea canescens* Torr. & Gray	1	
Geranium	*Geranium caespitosum*	*Geranium caespitosum* James	1	
Geranium		*Geranium* L.	1	
Gilia		*Gilia* Ruiz & Pavon	1	
Grayia	*Grayia spinosa*	*Grayia spinosa* (Hook.) Moq.	2	
Gutierrezia	*Gutierrezia microcephala*	*Gutierrezia microcephala* (DC.) Gray	19	1
Gutierrezia	*Gutierrezia sarothrae*	*Gutierrezia sarothrae* (Pursh) Britt. & Rusby	77	2
Helianthella	*Helianthella uniflora*	*Helianthella uniflora* (Nutt.) Torr. & Gray	5	
Helianthus	*Helianthus petiolaris*	*Helianthus petiolaris* Nutt.	1	
Hesperodoria	*Haplopappus scopulorum*	*Hesperodoria scopularum* (M.E. Jones) Greene	3	
Hesperostipa	*Stipa comata*	*Hesperostipa comata* ssp. *comata* (Trin. & Rupr.) Barkworth	30	2
Heuchera	*Heuchera rubescens*	*Heuchera rubescens* Torr.	1	
Heuchera	*Heuchera rubescens*	*Heuchera rubescens* var. *versicolor* (Greene) M.G. Stewart	2	
Hilaria		*Pleuraphis jamesii* Torr.	26	
Holodiscus	*Holodiscus dumosus*	*Holodiscus dumosus* (Nutt. ex Hook.) Heller	2	
Hordeum	*Hordeum brachyantherum*	*Hordeum brachyantherum* Nevski	1	
Hydrophyllum	*Hydrophyllum occidentale*	*Hydrophyllum occidentale* (S. Wats.) Gray	3	
Hymenopappus	*Hymenopappus filifolius*	*Hymenopappus filifolius* Hook.	20	
Hymenopappus	*Hymenopappus filifolius*	*Hymenopappus* L'Her.	1	
Hypochaeris	*Hypochaeris radicata*	*Hypochaeris radicata* L.	1	
Ipomoea	*Ipomoea purpurea*	*Ipomoea purpurea* (L.) Roth	1	
Ipomopsis	*Ipomopsis aggregata*	*Ipomopsis aggregata* (Pursh) V. Grant	3	
Ipomopsis	*Ipomopsis aggregata*	*Ipomopsis arizonica* (Greene) Wherry	1	
Ipomopsis	*Ipomopsis congesta*	*Ipomopsis congesta* ssp. *congesta* (Hook.) V. Grant	5	
Ipomopsis	*Ipomopsis congesta*	*Ipomopsis congesta* ssp. *frutescens* (Rydb.) Day	1	
Ivesia	*Ivesia sabulosa*	*Ivesia sabulosa* (M.E. Jones) Keck	3	
Juncus	*Juncus arcticus*	*Juncus balticus* Willd.	4	1
Juncus	*Juncus ensifolius*	*Juncus ensifolius* Wikstr.	2	
Juncus	*Juncus longistylis*	*Juncus longistylis* Torr.	3	
Juncus	*Juncus tenuis*	*Juncus tenuis* Willd.	3	
Juncus	*Juncus torreyi*	*Juncus torreyi* Coville	1	
Juncus		*Juncus* L.	2	1
Juniperus	*Juniperus osteosperma*	*Juniperus osteosperma* (Torr.) Little	104	12
Juniperus	*Juniperus scopulorum*	*Juniperus scopulorum* Sarg.	31	16
Juniperus		*Juniperus* L.	1	
Kelloggia	*Kelloggia galioides*	*Kelloggia galioides* Torr.	4	
Koeleria	*Koeleria macrantha*	*Koeleria macrantha* (Ledeb.) J.A. Schultes	6	
Krameria		*Krameria* L.	1	

Genus	**Species**	**Database Name**	**#In**	**#Out**
Lactuca	*Lactuca serriola*	*Lactuca serriola* L.	2	
Lactuca		*Lactuca* L.	3	
Lathyrus	*Lathyrus brachycalyx*	*Lathyrus brachycalyx* Rydb.	1	
Lathyrus		*Lathyrus* L.	3	
Lathyrus		*Lathyrus* L. ? *Vicia*?	1	
Lepidium		*Lepidium* L.	3	
Lepidium		*Lupidium* species	1	
Leptosiphon	*Linanthastrum nuttallii*	*Linanthus nuttallii ssp. nuttallii* (Gray) Greene ex Milliken	1	
Linanthus	*Leptodactylon watsonii*	*Leptodactylon watsonii* (Gray) Rydb.	1	
Linaria	*Linaria dalmatica*	*Linaria dalmatica* (L.) P. Mill.	2	
Linum	*Linum perenne*	*Linum perenne* L.	4	
Linum		*Linum* L.	4	
Lomatium	*Lomatium graveolens*	*Lomatium graveolens* (S. Wats.) Dorn & Hartman	1	
Lomatium		*Lomatium* Raf.	3	
Lotus	*Lotus rigidus*	*Lotus rigidus* (Benth.) Greene	2	
Lotus	*Lotus utahensis*	*Lotus utahensis* Ottley	23	
Lotus		*Lotus* L.	5	
Lupinus	*Lupinus argenteus*	*Lupinus argenteus* Pursh	15	
Lupinus	*Lupinus concinnus*	*Lupinus concinnus* J.G. Agardh	1	
Lupinus	*Lupinus sericeus*	*Lupinus sericeus* Pursh	2	
Lupinus		*Lupinus* L.	18	
Luzula	*Luzula campestris*	*Luzula campestris* (L.) DC.	1	
Luzula	*Luzula parviflora*	*Luzula parviflora* (Ehrh.) Desv.	4	
Lycium	*Lycium pallidum*	*Lycium pallidum* Miers	4	
Lycium		*Lycium* L.	0	1
Lygodesmia	*Lygodesmia juncea*	*Lygodesmia juncea* (Pursh) D. Don ex Hook.	1	
Lygodesmia		skeletonweed	1	
Machaeranthera	*Haplopappus gracilis*	*Machaeranthera gracilis* (Nutt.) Shinners	2	
Machaeranthera	*Machaeranthera canescens*	*Machaeranthera canescens* (Pursh) Gray	18	
Machaeranthera		*Machaeranthera* Nees	5	
Mahonia	*Mahonia repens*	*Mahonia repens* (Lindl.) G. Don	39	
Maianthemum	*Smilacina racemosa*	*Maianthemum racemosum* ssp. *racemosum* (L.) Link	6	
Maianthemum	*Smilacina stellata*	*Maianthemum stellatum* (L.) Link	9	
Medicago	*Medicago lupulina*	*Medicago lupulina* L.	2	
Melilotus	*Melilotus officinalis*	*Melilotus officinalis* (L.) Lam.	14	
Mentha	*Mentha arvensis*	*Mentha arvensis* L.	3	
Mentha	*Mentha piperita*	*Mentha X piperita* L. (pro sp.)	1	
Mertensia	*Mertensia arizonica*	*Mertensia arizonica* Greene	10	
Mertensia		*Mertensia* Roth	3	
Mirabilis	*Mirabilis multiflora*	*Mirabilis multiflora* (Torr.) Gray	3	
Monardella	*Monardella odoratissima*	*Monardella odoratissima* Benth.	1	
Muhlenbergia	*Muhlenbergia asperifolia*	*Muhlenbergia asperifolia* (Nees & Meyen ex Trin.) Parodi	3	
Muhlenbergia	*Muhlenbergia montana*	*Muhlenbergia montana* (Nutt.) A.S. Hitchc.	8	
Muhlenbergia	*Muhlenbergia pauciflora*	*Muhlenbergia pauciflora* Buckl.	1	
Muhlenbergia	*Muhlenbergia porteri*	*Muhlenbergia porteri* Scribn. ex Beal	3	
Muhlenbergia	*Muhlenbergia racemosa*	*Muhlenbergia racemosa* (Michx.) B.S.P.	2	
Muhlenbergia	*Muhlenbergia thurberi*	*Muhlenbergia thurberi* Rydb.	1	

Genus	Species	Database Name	#In	#Out
Muhlenbergia	*Muhlenbergia wrightii*	*Muhlenbergia wrightii* Vasey ex Coult.	1	
Muhlenbergia		*Muhlenbergia* Schreb.	5	
Nassella	*Stipa viridula*	*Nassella viridula* (Trin.) Barkworth	2	
Nasturtium	*Nasturtium officinale*	*Rorippa nasturtium-aquaticum* (L.) Hayek	1	
Nicotiana	*Nicotiana attenuata*	*Nicotiana attenuata* Torr. ex S. Wats.	1	
Oenothera	*Oenothera caespitosa*	*Oenothera cespitosa* Nutt.	1	
Oenothera	*Oenothera flava*	*Oenothera flava* (A. Nels.) Garrett	1	
Oenothera	*Oenothera howardii*	*Oenothera howardii* (A. Nels.) W.L. Wagner	1	
Oenothera	*Oenothera pallida*	*Oenothera pallida* Lindl.	5	
Oenothera		*Oenothera* L.	7	
Opuntia	*Opuntia basilaris*	*Opuntia basilaris* Engelm. & Bigelow	8	1
Opuntia	*Opuntia chlorotica*	*Opuntia chlorotica* Engelm. & Bigelow	3	
Opuntia	*Opuntia echinocarpa*	*Opuntia echinocarpa* Engelm. & Bigelow	2	
Opuntia	*Opuntia erinacea*	*Opuntia erinacea* Engelm. & Bigelow ex Engelm.	5	
Opuntia	*Opuntia macrorhiza*	*Opuntia macrorhiza* Engelm.	93	2
Opuntia	*Opuntia phaeacantha*	*Opuntia engelmannii* Salm-Dyck	1	
Opuntia	*Opuntia phaeacantha*	*Opuntia phaeacantha* Engelm.	35	1
Opuntia	*Opuntia polyacantha*	*Opuntia polyacantha* Haw.	4	
Opuntia	*Opuntia whipplei*	*Opuntia whipplei* Engelm. & Bigelow	4	2
Opuntia		*Opuntia* P. Mill.	3	
Osmorhiza	*Osmorhiza depauperata*	*Osmorhiza depauperata* Phil.	2	
Osmorhiza	*Osmorhiza occidentalis*	*Osmorhiza occidentalis* (Nutt. ex Torr. & Gray) Torr.	6	
Osmorhiza		*Osmorhiza* Raf.	1	
Oxytropis		*Oxytropis* DC.	1	
Pachystima	*Pachystima myrsinites*	*Paxistima myrsinites* (Pursh) Raf.	38	
Penstemon	*Penstemon caespitosus*	*Penstemon caespitosus* Nutt. ex Gray	9	
Penstemon	*Penstemon caespitosus*	*Penstemon tusharensis* N. Holmgren	1	
Penstemon	*Penstemon eatonii*	*Penstemon eatonii* Gray	13	
Penstemon	*Penstemon higginsii*	*Penstemon leonardii* Rydb.	6	
Penstemon	*Penstemon higginsii*	*Penstemon leonardii* var. *higginsii* Neese	1	
Penstemon	*Penstemon humilis*	*Penstemon humilis* Nutt. ex Gray	3	
Penstemon	*Penstemon lentus*	*Penstemon lentus* Pennell	1	
Penstemon	*Penstemon linarioides*	*Penstemon linarioides* Gray	9	
Penstemon	*Penstemon pachyphyllus*	*Penstemon pachyphyllus* Gray ex Rydb.	2	
Penstemon	*Penstemon palmeri*	*Penstemon palmeri* Gray	13	2
Penstemon	*Penstemon rostriflorus*	*Penstemon rostriflorus* Kellogg	2	
Penstemon		*Penstemon* Schmidel	35	
Peraphyllum	*Peraphyllum ramosissimum*	*Peraphyllum ramosissimum* Nutt.	8	
Petradoria	*Petradoria pumila*	*Petradoria pumila* (Nutt.) Greene	7	
Petrophytum	*Petrophytum caespitosum*	*Petrophyton caespitosum* (Nutt.) Rydb.	3	
Phacelia	*Phacelia heterophylla*	*Phacelia heterophylla* Pursh	21	
Phacelia		*Phacelia* Juss.	4	
Phleum	*Phleum pratense*	*Phleum pratense* L.	1	
Phlox	*Phlox austromontana*	*Phlox austromontana* Coville	30	
Phlox	*Phlox hoodii*	*Phlox hoodii* Richards.	4	
Phlox	*Phlox longifolia*	*Phlox longifolia* Nutt.	1	

Genus	Species	Database Name	#In	#Out
Phlox	*Phlox pulvinata*	*Phlox caespitosa* Nutt.	1	
Phlox		*Phlox* L.	7	
Phoradendron	*Phoradendron juniperinum*	*Phoradendron juniperinum* Engelm.	2	
Phragmites	*Phragmites australis*	*Phragmites australis* (Cav.) Trin. ex Steud.	1	
Physalis	*Physalis hederifolia*	*Physalis hederifolia* Gray	1	
Physalis	*Physalis heterophylla*	*Physalis heterophylla* Nees	1	
Physaria	*Physaria chambersii*	*Physaria chambersii* Rollins	6	
Physaria	*Physaria newberryi*	*Physaria newberryi* Gray	1	
Physaria		*Physaria* (Nutt. ex Torr. & Gray) Gray	2	
Pinus	*Pinus edulis*	*Pinus edulis* Engelm.	43	3
Pinus	*Pinus edulis*	*Pinus edulis x monophylla* Engelm.	4	
Pinus	*Pinus monophylla*	*Pinus monophylla* Torr. & Frem.	52	5
Pinus	*Pinus ponderosa*	*Pinus ponderosa* P.& C. Lawson	52	14
Plagiobothrys	*Plagiobothrys tenellus*	*Plagiobothrys tenellus* (Nutt. ex Hook.) Gray	1	
Plantago	*Plantago patagonica*	*Plantago patagonica* Jacq.	3	
Pluchea	*Pluchea sericea*	*Pluchea sericea* (Nutt.) Coville	2	
Poa	*Poa fendleriana*	*Poa fendleriana* (Steud.) Vasey	147	1
Poa	*Poa pratensis*	*Poa pratensis* L.	43	
Poa	*Poa secunda*	*Poa secunda* J. Presl	12	
Poa		*Poa* L.	8	
Poa		*Poa*2 L.	1	
Poaceae spp.		unknown grass	3	
Polygonum	*Polygonum douglasii*	*Polygonum douglasii* Greene	7	
Polygonum		*Polygonum* L.	3	
Polypodium	*Polypodium hesperium*	*Polypodium hesperium* Maxon	1	
Polypogon		*Polypogon* Desf.	1	
Populus	*Populus angustifolia*	*Populus angustifolia* James	1	
Populus	*Populus fremontii*	*Populus fremontii* S. Wats.	18	2
Populus	*Populus tremuloides*	*Populus tremuloides* Michx.	10	
Potentilla	*Potentilla glandulosa*	*Potentilla glandulosa* Lindl.	1	
Prosopis	*Prosopis glandulosa*	*Prosopis glandulosa* Torr.	1	
Prunus	*Prunus virginiana*	*Prunus virginiana* L.	14	
Prunus		*Prunus* L.	1	
Pseudotsuga	*Pseudotsuga menziesii*	*Pseudotsuga menziesii* (Mirbel) Franco	18	1
Psoralidium		*Psoralidium* Rydb.	1	
Psorothamnus	*Psorothamnus fremontii*	*Psorothamnus fremontii* (Torr. ex Gray) Barneby	6	2
Psorothamnus	*Psorothamnus fremontii*	*Psorothamnus fremontii* var. *fremontii* (Torr. ex Gray) Barneby	1	
Pteridium	*Pteridium aquilinum*	*Pteridium aquilinum* (L.) Kuhn	4	
Pterospora	*Pterospora andromedea*	*Pterospora andromedea* Nutt.	1	
Puccinellia	*Puccinellia distans*	*Puccinellia distans* (Jacq.) Parl.	1	
Purshia	*Purshia mexicana*	*Purshia mexicana* (D. Don) Henrickson	10	1
Purshia	*Purshia mexicana*	*Purshia stansburiana* (Torr.) Henrickson	6	
Purshia	*Purshia tridentata*	*Purshia tridentata* (Pursh) DC.	46	1
Purshia		*Purshia* DC. ex Poir.	1	
Quercus	*Quercus gambelii*	*Quercus gambelii* Nutt.	160	3
Quercus	*Quercus turbinella*	*Quercus turbinella* Greene	38	1

Genus	Species	Database Name	#In	#Out
Rhus	*Rhus aromatica*	*Rhus aromatica* Ait.	6	3
Rhus	*Rhus aromatica*	*Rhus trilobata* Nutt.	13	2
Rhus	*Rhus aromatica*	*Rhus trilobata* var. *trilobata* Nutt.	7	2
Rosa	*Rosa woodsii*	*Rosa woodsii* Lindl.	16	
Rumex	*Rumex acetosella*	*Rumex acetosella* L.	2	
Rumex	*Rumex hymenosepalus*	*Rumex hymenosepalus* Torr.	2	
Salix	*Salix eriocephala*	*Salix ligulifolia* (Ball) Ball ex Schneid.	2	
Salix	*Salix exigua*	*Salix exigua* Nutt.	11	1
Salix	*Salix gooddingii*	*Salix gooddingii* Ball	1	1
Salix	*Salix lasiolepis*	*Salix lasiolepis* Benth.	1	
Salix	*Salix lucida*	*Salix lucida* Muhl.	1	
Salix	*Salix lucida*	*Salix lucida* ssp. *lasiandra* (Benth.) E. Murr.	1	
Salix	*Salix scouleriana*	*Salix scouleriana* Barratt ex Hook.	0	1
Salix		*Salix* L.	3	1
Salsola	*Salsola tragus*	*Salsola kali* ssp. *tragus* (L.) Celak.	1	
Salvia	*Salvia dorrii*	*Salvia dorrii* (Kellogg) Abrams	4	1
Sambucus		*Sambucus* L.	1	
Schizachyrium	*Schizachyrium scoparium*	*Schizachyrium scoparium* (Michx.) Nash	1	
Scirpus	*Scirpus americanus*	*Schoenoplectus americanus* (Pers.) Volk. ex Schinz & R. Keller	1	
Scirpus	*Scirpus validus*	*Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla	1	
Scirpus		*Scirpus* L.	1	
Senecio	*Senecio eremophilus*	*Senecio eremophilus* Richards.	3	
Senecio	*Senecio integerrimus*	*Senecio integerrimus* Nutt.	1	
Senecio	*Senecio multilobatus*	*Senecio multilobatus* Torr. & Gray ex Gray	30	
Senecio	*Senecio spartioides*	*Senecio spartioides* Torr. & Gray	16	
Senecio		*Senecio* L.	13	
Shepherdia	*Shepherdia rotundifolia*	*Shepherdia rotundifolia* Parry	11	
Sisymbrium	*Sisymbrium altissimum*	*Sisymbrium altissimum* L.	3	
Sisymbrium		*Sisymbrium* L.	1	
Sisyrinchium	*Sisyrinchium demissum*	*Sisyrinchium demissum* Greene	2	
Solanum	*Solanum elaeagnifolium*	*Solanum elaeagnifolium* Cav.	1	
Solidago	*Solidago velutina*	*Solidago velutina* DC.	8	
Solidago		*Solidago* L.	1	
Sorghastrum	*Sorghastrum nutans*	*Sorghastrum nutans* (L.) Nash	2	
Sphaeralcea	*Sphaeralcea ambigua*	*Sphaeralcea ambigua* Gray	2	
Sphaeralcea	*Sphaeralcea coccinea*	*Sphaeralcea coccinea* (Nutt.) Rydb.	10	2
Sphaeralcea	*Sphaeralcea grossulariifolia*	*Sphaeralcea grossulariifolia* (Hook. & Arn.) Rydb.	3	
Sphaeralcea		*Sphaeralcea* St.-Hil.	5	1
Sphaeromeria	*Sphaeromeria ruthiae*	*Sphaeromeria ruthiae* Holmgren, Shultz & Lowrey	1	1
Sporobolus	*Sporobolus cryptandrus*	*Sporobolus cryptandrus* (Torr.) Gray	56	
Sporobolus		*Sporobolus* R. Br.	1	
Stanleya	*Stanleya pinnata*	*Stanleya pinnata* (Pursh) Britt.	3	
Stellaria	*Stellaria jamesiana*	*Pseudostellaria jamesiana* (Torr.) W.A. Weber & R.L. Hartman	3	
Stellaria	*Stellaria media*	*Stellaria media* (L.) Vill.	1	
Stellaria		*Stellaria* L.	2	

Genus	Species	Database Name	#In	#Out
Stephanomeria	*Stephanomeria exigua*	*Stephanomeria exigua* Nutt.	1	
Stephanomeria	*Stephanomeria tenuifolia*	*Stephanomeria tenuifolia* (Raf.) Hall	1	
Stephanomeria		*Stephanomeria* Nutt.	2	
Stipinae spp.		*Stipa* L.	6	
Stipinae spp.		*Stipa* L. (comata or lettermanii)	1	
Streptanthus	*Streptanthus cordatus*	*Streptanthus cordatus* Nutt.	3	
Swertia	*Swertia radiata*	*Frasera speciosa* Dougl. ex Griseb.	11	
Symphoricarpos	*Symphoricarpos longiflorus*	*Symphoricarpos longiflorus* Gray	2	
Symphoricarpos	*Symphoricarpos oreophilus*	*Symphoricarpos oreophilus* Gray	78	
Symphyotrichum	*Aster ascendens*	*Aster ascendens* Lindl.	1	
Tamarix	*Tamarix chinensis*	*Tamarix ramosissima* Ledeb.	8	2
Taraxacum	*Taraxacum officinale*	*Taraxacum officinale* G.H. Weber ex Wiggers	6	
Tetradymia	*Tetradymia axillaris*	*Tetradymia axillaris* A. Nels.	1	
Tetradymia	*Tetradymia canescens*	*Tetradymia canescens* DC.	9	1
Thalictrum	*Thalictrum fendleri*	*Thalictrum fendleri* Engelm. ex Gray	15	
Thalictrum		*Thalictrum* L.		1
Thermopsis	*Thermopsis montana*	*Thermopsis montana* Nutt.	2	
Townsendia		*Townsendia* Hook.	2	
Toxicodendron	*Toxicodendron rydbergii*	*Toxicodendron rydbergii* (Small ex Rydb.) Greene	2	
Tradescantia	*Tradescantia occidentalis*	*Tradescantia occidentalis* (Britt.) Smyth	13	
Tragia	*Tragia ramosa*	*Tragia ramosa* Torr.	1	
Tragopogon	*Tragopogon dubius*	*Tragopogon dubius* Scop.	21	
Tribulus	*Tribulus terrestris*	*Tribulus terrestris* L.	2	
Trifolium	*Trifolium gymnocarpon*	*Trifolium gymnocarpon* Nutt.	1	
Trifolium	*Trifolium longipes*	*Trifolium longipes* Nutt.	3	
Trifolium		*Trifolium* L.	3	
Typha	*Typha domingensis*	*Typha angustifolia* L.	2	
Typha	*Typha domingensis*	*Typha domingensis* Pers.	1	
Verbascum	*Verbascum thapsus*	*Verbascum thapsus* L.	12	
Verbena	*Verbena bracteata*	*Verbena bracteata* Lag. & Rodr.	2	
Vicia	*Vicia americana*	*Vicia americana* Muhl. ex Willd.	50	
Vicia		*Vicia* L.	5	
Viguiera	*Viguiera multiflora*	*Heliomeris multiflora* var. *multiflora* Nutt.	9	
Viola	*Viola purpurea*	*Viola charlestonensis* M.S. Baker & J.C. Clausen ex Clokey	1	
Viola		*Viola* L.	1	
Vitis	*Vitis arizonica*	*Vitis arizonica* Engelm.	4	
Wyethia	*Wyethia arizonica*	*Wyethia arizonica* Gray	2	
Yucca	*Yucca baccata*	*Yucca baccata* Torr.	19	1
Yucca	*Yucca utahensis*	*Yucca elata* var. *utahensis* (McKelvey) Reveal	65	8

APPENDIX 3.2

Results of niche overlap significance tests comparing congeneric species of vascular plants recorded in the USGS-NPS vegetation characterization of Zion National Park, Utah (Cogan et al. 2004). Null model distributions of beta niche overlap (across habitats) and alpha niche overlap (across plots within habitats), using both presence and cover measures, were built through randomization and compared with observed overlap values. Prob=probabilities ranging from -1 (more segregated than expected) to 1 (more aggregated than expected). Sig=cases of statistically signification segregation (-) or aggregation (+). Families are listed in phylogenetic sequence of Fig. 3.1.

		Beta Niche				**Alpha Niche**			
		Presence		**Cover**		**Presence**		**Cover**	
Family	**Congeneric Pair**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Equisetaceae	*Equisetum arvense / hyemale*	1.00	+	0.88		0.55		0.55	
Equisetaceae	*Equisetum arvense / laevigatum*	0.98	+	1.00	+	0.00		0.00	
Equisetaceae	*Equisetum arvense / variegatum*	0.97	+	0.75		0.00		0.00	
Equisetaceae	*Equisetum hyemale / laevigatum*	0.86		0.90		0.00		0.00	
Equisetaceae	*Equisetum hyemale / variegatum*	0.81		0.65		0.00		0.00	
Equisetaceae	*Equisetum laevigatum / variegatum*	0.98	+	0.71		0.00		0.00	
Cupressaceae	*Juniperus osteosperma / scopulorum*	-1.00	-	-0.90		-0.93		-0.15	
Pinaceae	*Pinus edulis / monophylla*	-0.94		-0.46		-1.00	-	-0.98	-
Pinaceae	*Pinus edulis / ponderosa*	-1.00	-	-1.00	-	-0.55		-0.95	-
Pinaceae	*Pinus monophylla / ponderosa*	-1.00	-	-1.00	-	-0.75		-0.92	
Ephedraceae	*Ephedra nevadensis / viridis*	-0.45		-0.98	-	-0.19		-0.80	
Cyperaceae	*Carex geyeri / microptera*	-0.47		-0.47		0.00		0.00	
Cyperaceae	*Carex geyeri / nebrascensis*	0.00		0.00		0.00		0.00	
Cyperaceae	*Carex geyeri / occidentalis*	-0.19		-0.52		0.00		0.00	
Cyperaceae	*Carex geyeri / rossii*	0.13		0.00		0.00		0.00	
Cyperaceae	*Carex geyeri / utriculata*	0.00		0.00		0.00		0.00	
Cyperaceae	*Carex microptera / nebrascensis*	1.00	+	0.99	+	0.50		0.79	
Cyperaceae	*Carex microptera / occidentalis*	-0.42		0.94		0.91		1.00	+
Cyperaceae	*Carex microptera / rossii*	-0.99	-	-0.99	-	0.00		0.00	
Cyperaceae	*Carex microptera / utriculata*	1.00	+	0.99	+	0.53		0.53	
Cyperaceae	*Carex nebrascensis / occidentalis*	0.10		0.90		0.00		0.00	
Cyperaceae	*Carex nebrascensis / rossii*	-0.79		-0.79		0.00		0.00	
Cyperaceae	*Carex nebrascensis / utriculata*	0.97	+	0.99	+	0.00		0.00	
Cyperaceae	*Carex occidentalis / rossii*	-0.03		-0.84		0.45		0.45	
Cyperaceae	*Carex occidentalis / utriculata*	0.03		0.90		0.75		0.90	
Cyperaceae	*Carex rossii / utriculata*	-0.79		-0.79		0.00		0.00	
Cyperaceae	*Scirpus americanus / validus*	0.87		0.87		0.00		0.00	
Juncaceae	*Juncus arcticus / ensifolius*	1.00	+	1.00	+	0.41		0.53	
Juncaceae	*Juncus arcticus / longistylis*	1.00	+	1.00	+	0.21		0.39	
Juncaceae	*Juncus arcticus / tenuis*	1.00	+	1.00	+	0.15		0.29	
Juncaceae	*Juncus arcticus / torreyi*	1.00	+	0.97	+	0.00		0.00	

		Beta Niche				Alpha Niche			
		Presence		Cover		Presence		Cover	
Family	**Congeneric Pair**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Juncaceae	*Juncus ensifolius / longistylis*	1.00	+	1.00	+	0.97	+	0.97	+
Juncaceae	*Juncus ensifolius / tenuis*	1.00	+	0.99	+	0.97	+	0.91	
Juncaceae	*Juncus ensifolius / torreyi*	0.96	+	0.93		0.00		0.00	
Juncaceae	*Juncus longistylis / tenuis*	1.00	+	1.00	+	1.00	+	1.00	+
Juncaceae	*Juncus longistylis / torreyi*	1.00	+	1.00	+	0.00		0.00	
Juncaceae	*Juncus tenuis / torreyi*	1.00	+	0.98	+	0.00		0.00	
Juncaceae	*Luzula campestris / parviflora*	1.00	+	1.00	+	0.00		0.00	
Poaceae	*Aristida purpurascens / purpurea*	-0.87		-0.94		0.00		0.00	
Poaceae	*Muhlenbergia asperifolia / montana*	-0.91		-0.91		0.00		0.00	
Poaceae	*Muhlenbergia asperifolia / pauciflora*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia asperifolia / porteri*	-0.43		-0.43		0.00		0.00	
Poaceae	*Muhlenbergia asperifolia / racemosa*	0.90		0.88		0.00		0.00	
Poaceae	*Muhlenbergia asperifolia / thurberi*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia asperifolia / wrightii*	1.00	+	0.98	+	0.00		0.00	
Poaceae	*Muhlenbergia montana / pauciflora*	-0.24		-0.24		0.00		0.00	
Poaceae	*Muhlenbergia montana / porteri*	-0.90		-0.90		0.00		0.00	
Poaceae	*Muhlenbergia montana / racemosa*	-0.73		-0.73		0.00		0.00	
Poaceae	*Muhlenbergia montana / thurberi*	-0.34		-0.34		0.00		0.00	
Poaceae	*Muhlenbergia montana / wrightii*	-0.35		-0.35		0.00		0.00	
Poaceae	*Muhlenbergia pauciflora / porteri*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia pauciflora / racemosa*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia pauciflora / thurberi*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia pauciflora / wrightii*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia porteri / racemosa*	-0.07		-0.07		0.00		0.00	
Poaceae	*Muhlenbergia porteri / thurberi*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia porteri / wrightii*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia racemosa / thurberi*	0.00		0.00		0.00		0.00	
Poaceae	*Muhlenbergia racemosa / wrightii*	0.87		0.87		0.00		0.00	
Poaceae	*Muhlenbergia thurberi / wrightii*	0.00		0.00		0.00		0.00	
Poaceae	*Bouteloua barbata / gracilis*	-0.81		-0.71		0.00		0.00	
Poaceae	*Stipa hymenoides / lettermanii*	-0.99	-	-0.09		0.17		0.73	
Poaceae	*Stipa hymenoides / nelsonii*	-0.98	-	-0.97	-	0.00		0.00	
Poaceae	*Stipa hymenoides / speciosa*	-0.70		-0.84		-0.30		-0.24	
Poaceae	*Stipa lettermanii / nelsonii*	-0.18		-0.66		0.46		0.46	
Poaceae	*Stipa lettermanii / speciosa*	-0.99	-	-0.99	-	0.00		0.00	
Poaceae	*Stipa nelsonii / speciosa*	-0.47		-0.47		0.00		0.00	
Poaceae	*Poa fendleriana / pratensis*	-1.00	-	-1.00	-	-0.94		-0.95	-
Poaceae	*Poa fendleriana / secunda*	-0.11		0.87		-0.55		0.46	
Poaceae	*Poa pratensis / secunda*	-1.00	-	-0.98	-	-0.39		-0.39	
Poaceae	*Festuca occidentalis / octoflora*	0.00		0.00		0.00		0.00	
Poaceae	*Agrostis exarata / stolonifera*	1.00	+	1.00	+	0.00		0.00	
Poaceae	*Bromus anomalus / diandrus*	0.22		0.01		0.00		0.00	
Poaceae	*Bromus anomalus / inermis*	-0.89		-0.91		0.00		0.00	
Poaceae	*Bromus anomalus / rubens*	-0.45		-0.63		0.00		0.00	
Poaceae	*Bromus anomalus / tectorum*	-0.96	-	0.45		0.03		0.05	

		Beta Niche				Alpha Niche			
		Presence		Cover		Presence		Cover	
Family	**Congeneric Pair**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Poaceae	*Bromus diandrus / inermis*	-0.99	-	-0.99	-	-0.07		-0.01	
Poaceae	*Bromus diandrus / rubens*	-0.17		-0.37		0.00		0.00	
Poaceae	*Bromus diandrus / tectorum*	-0.98	-	-0.85		0.76		0.75	
Poaceae	*Bromus inermis / rubens*	-0.95	-	-0.99	-	0.00		0.00	
Poaceae	*Bromus inermis / tectorum*	-1.00	-	-1.00	-	-0.56		-0.65	
Poaceae	*Bromus rubens / tectorum*	-0.15		-0.27		0.77		0.27	
Poaceae	*Elymus canadensis / elymoides*	-0.99	-	-0.98	-	0.00		0.00	
Poaceae	*Elymus canadensis / glaucus*	0.00		0.00		0.00		0.00	
Poaceae	*Elymus canadensis / hispidus*	0.00		0.00		0.00		0.00	
Poaceae	*Elymus canadensis / lanceolatus*	-0.43		-0.65		0.00		0.00	
Poaceae	*Elymus canadensis / repens*	-0.57		-0.57		0.00		0.00	
Poaceae	*Elymus canadensis / smithii*	0.63		0.40		0.00		0.00	
Poaceae	*Elymus canadensis / spicatus*	0.00		0.00		0.00		0.00	
Poaceae	*Elymus elymoides / glaucus*	-0.71		0.03		0.00		0.00	
Poaceae	*Elymus elymoides / hispidus*	-0.66		-0.42		0.00		0.00	
Poaceae	*Elymus elymoides / lanceolatus*	-0.99	-	-0.97	-	0.38		0.95	+
Poaceae	*Elymus elymoides / repens*	-0.50		0.87		-0.58		-0.58	
Poaceae	*Elymus elymoides / smithii*	-1.00	-	-1.00	-	-0.36		-0.36	
Poaceae	*Elymus elymoides / spicatus*	0.92		0.93		0.48		0.91	
Poaceae	*Elymus glaucus / hispidus*	0.00		0.00		0.00		0.00	
Poaceae	*Elymus glaucus / lanceolatus*	-0.37		-0.36		0.00		0.00	
Poaceae	*Elymus glaucus / repens*	0.18		0.50		0.00		0.00	
Poaceae	*Elymus glaucus / smithii*	-0.32		-0.34		0.00		0.00	
Poaceae	*Elymus glaucus / spicatus*	0.00		0.00		0.00		0.00	
Poaceae	*Elymus hispidus / lanceolatus*	0.85		0.88		0.00		0.00	
Poaceae	*Elymus hispidus / repens*	-0.41		-0.14		0.00		0.00	
Poaceae	*Elymus hispidus / smithii*	0.40		0.49		0.00		0.00	
Poaceae	*Elymus hispidus / spicatus*	0.00		0.00		0.00		0.00	
Poaceae	*Elymus lanceolatus / repens*	-0.69		-0.68		0.00		0.00	
Poaceae	*Elymus lanceolatus / smithii*	-0.15		0.14		-0.10		-0.10	
Poaceae	*Elymus lanceolatus / spicatus*	0.24		-0.14		0.00		0.00	
Poaceae	*Elymus repens / smithii*	-0.91		-0.86		0.61		0.91	
Poaceae	*Elymus repens / spicatus*	0.97	+	0.87		0.00		0.00	
Poaceae	*Elymus smithii / spicatus*	-0.33		-0.33		0.00		0.00	
Ruscaceae	*Smilacina racemosa / stellata*	-0.38		-0.73		-0.24		-0.24	
Agavaceae	*Yucca baccata / utahensis*	-0.98	-	0.50		-0.43		0.55	
Ranunculaceae	*Clematis columbiana / ligusticifolia*	0.17		0.43		0.00		0.00	
Fagaceae	*Quercus gambelii / turbinella*	-1.00	-	-1.00	-	-0.98	-	-0.99	-
Rosaceae	*Cercocarpus intricatus / ledifolius*	-0.39		0.73		0.00		0.00	
Rosaceae	*Cercocarpus intricatus / montanus*	-0.93		0.62		-0.45		-0.35	
Rosaceae	*Cercocarpus ledifolius / montanus*	0.68		0.80		0.13		0.42	
Rosaceae	*Purshia mexicana / tridentata*	-0.69		0.85		-0.96	-	-0.95	
Rosaceae	*Amelanchier alnifolia / utahensis*	-1.00	-	-0.89		-0.97	-	-0.33	
Rhamnaceae	*Ceanothus fendleri / martinii*	0.83		0.35		0.00		0.00	

		Beta Niche				Alpha Niche			
		Presence		**Cover**		**Presence**		**Cover**	
Family	**Congeneric Pair**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Fabaceae	*Lupinus argenteus / concinnus*	0.42		0.62		0.00		0.00	
Fabaceae	*Lupinus argenteus / sericeus*	-0.76		-0.57		0.00		0.00	
Fabaceae	*Lupinus concinnus / sericeus*	0.00		0.00		0.00		0.00	
Fabaceae	*Lotus rigidus / utahensis*	0.18		-0.37		0.00		0.00	
Fabaceae	*Astragalus flavus / subcinereus*	0.00		0.00		0.00		0.00	
Fabaceae	*Trifolium gymnocarpon / longipes*	0.00		0.00		0.00		0.00	
Euphorbiaceae	*Chamaesyce albomarginata / fendleri*	-0.19		-0.19		0.00		0.00	
Euphorbiaceae	*Chamaesyce albomarginata / glyptosperma*	0.71		0.71		0.00		0.00	
Euphorbiaceae	*Chamaesyce albomarginata / parryi*	0.00		0.00		0.00		0.00	
Euphorbiaceae	*Chamaesyce fendleri / glyptosperma*	0.34		0.57		0.00		0.00	
Euphorbiaceae	*Chamaesyce fendleri / parryi*	0.19		0.19		0.00		0.00	
Euphorbiaceae	*Chamaesyce glyptosperma / parryi*	0.00		0.00		0.00		0.00	
Salicaceae	*Populus angustifolia / fremontii*	1.00	+	1.00	+	0.00		0.46	
Salicaceae	*Populus angustifolia / tremuloides*	-0.44		-0.44		0.00		0.00	
Salicaceae	*Populus fremontii / tremuloides*	-1.00	-	-1.00	-	0.00		0.00	
Salicaceae	*Salix eriocephala / exigua*	1.00	+	1.00	+	0.00		0.00	
Salicaceae	*Salix eriocephala / gooddingii*	0.99	+	0.90		0.00		0.00	
Salicaceae	*Salix eriocephala / lasiolepis*	0.88		0.88		0.00		0.00	
Salicaceae	*Salix eriocephala / lucida*	0.99	+	0.92		0.00		0.00	
Salicaceae	*Salix eriocephala / scouleriana*[1]	0.00				0.00			
Salicaceae	*Salix exigua / gooddingii*	1.00	+	1.00	+	0.07		0.00	
Salicaceae	*Salix exigua / lasiolepis*	1.00	+	1.00	+	0.00		0.00	
Salicaceae	*Salix exigua / lucida*	1.00	+	1.00	+	0.07		0.50	
Salicaceae	*Salix exigua / scouleriana*[1]	-0.54				0.00			
Salicaceae	*Salix gooddingii / lasiolepis*	0.99	+	0.92		0.00		0.00	
Salicaceae	*Salix gooddingii / lucida*	0.99	+	1.00	+	0.76		0.94	
Salicaceae	*Salix gooddingii / scouleriana*[1]	0.00				0.00			
Salicaceae	*Salix lasiolepis / lucida*	0.98	+	0.92		0.00		0.00	
Salicaceae	*Salix lasiolepis / scouleriana*[1]	0.00				0.00			
Salicaceae	*Salix lucida / scouleriana*[1]	0.00				0.00			
Brassicaceae	*Arabis holboellii / perennans*	0.73		0.73		0.00		0.00	
Brassicaceae	*Physaria chambersii / newberryi*	0.32		0.32		0.00		0.00	
Malvaceae	*Sphaeralcea ambigua / coccinea*	-0.09		0.49		0.00		0.00	
Malvaceae	*Sphaeralcea ambigua / grossulariifolia*	-0.09		-0.09		0.00		0.00	
Malvaceae	*Sphaeralcea coccinea / grossulariifolia*	-0.07		-0.24		0.00		0.00	
Sapindaceae	*Acer grandidentatum / negundo*	-1.00	-	-1.00	-	0.84		0.46	
Onagraceae	*Epilobium brachycarpum / latifolia*	0.76		0.76		0.00		0.00	
Onagraceae	*Oenothera caespitosa / flava*	0.00		0.00		0.00		0.00	
Onagraceae	*Oenothera caespitosa / howardii*	0.00		0.00		0.00		0.00	
Onagraceae	*Oenothera caespitosa / pallida*	0.00		0.00		0.00		0.00	
Onagraceae	*Oenothera flava / howardii*	0.00		0.00		0.00		0.00	
Onagraceae	*Oenothera flava / pallida*	-0.01		-0.01		0.00		0.00	
Onagraceae	*Oenothera howardii / pallida*	0.42		0.42		0.00		0.00	

		Beta Niche				Alpha Niche			
		Presence		Cover		Presence		Cover	
Family	**Congeneric Pair**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Polygonaceae	*Eriogonum corymbosum / fasciculatum*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum corymbosum / flavum*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum corymbosum / inflatum*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum corymbosum / microthecum*	0.01		0.12		0.00		0.00	
Polygonaceae	*Eriogonum corymbosum / ovalifolium*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum corymbosum / panguicense*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum corymbosum / racemosum*	-0.21		-0.21		0.00		0.00	
Polygonaceae	*Eriogonum corymbosum / umbellatum*	-0.55		-0.63		0.00		0.00	
Polygonaceae	*Eriogonum fasciculatum / flavum*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum fasciculatum / inflatum*	0.32		0.32		0.00		0.00	
Polygonaceae	*Eriogonum fasciculatum / microthecum*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum fasciculatum / ovalifolium*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum fasciculatum / panguicense*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum fasciculatum / racemosum*	-0.77		-0.77		0.00		0.00	
Polygonaceae	*Eriogonum fasciculatum / umbellatum*	-0.25		0.16		0.63		0.63	
Polygonaceae	*Eriogonum flavum / inflatum*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum flavum / microthecum*	0.98	+	0.97	+	0.00		0.00	
Polygonaceae	*Eriogonum flavum / ovalifolium*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum flavum / panguicense*	0.57		0.83		0.00		0.00	
Polygonaceae	*Eriogonum flavum / racemosum*	0.85		0.85		0.00		0.00	
Polygonaceae	*Eriogonum flavum / umbellatum*	1.00	+	0.98	+	0.00		0.00	
Polygonaceae	*Eriogonum inflatum / microthecum*	-0.72		-0.59		0.00		0.00	
Polygonaceae	*Eriogonum inflatum / ovalifolium*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum inflatum / panguicense*	0.28		0.05		0.00		0.00	
Polygonaceae	*Eriogonum inflatum / racemosum*	-0.33		-0.33		0.00		0.00	
Polygonaceae	*Eriogonum inflatum / umbellatum*	-0.71		-0.20		0.00		0.00	
Polygonaceae	*Eriogonum microthecum / ovalifolium*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum microthecum / panguicense*	0.45		0.98	+	0.00		0.00	
Polygonaceae	*Eriogonum microthecum / racemosum*	-0.13		0.33		0.00		0.00	
Polygonaceae	*Eriogonum microthecum / umbellatum*	0.68		0.75		0.00		0.00	
Polygonaceae	*Eriogonum ovalifolium / panguicense*	0.00		0.00		0.00		0.00	
Polygonaceae	*Eriogonum ovalifolium / racemosum*	-0.74		-0.74		0.00		0.00	
Polygonaceae	*Eriogonum ovalifolium / umbellatum*	-0.76		-0.77		0.00		0.00	
Polygonaceae	*Eriogonum panguicense / racemosum*	0.96	+	0.99	+	0.00		0.00	
Polygonaceae	*Eriogonum panguicense / umbellatum*	0.81		1.00	+	0.00		0.00	
Polygonaceae	*Eriogonum racemosum / umbellatum*	-0.29		0.25		0.99	+	0.97	+
Polygonaceae	*Rumex acetosella / hymenosepalus*	0.00		0.00		0.00		0.00	
Amaranthaceae	*Chenopodium album / fremontii*	-0.36		-0.36		0.00		0.00	
Caryophyllaceae	*Arenaria fendleri / macradenia*	0.49		0.96	+	0.04		0.60	
Caryophyllaceae	*Stellaria jamesiana / media*	0.00		0.00		0.00		0.00	
Cactaceae	*Echinocereus engelmannii / triglochidiatus*	1.00	+	1.00	+	-0.45		-0.31	
Cactaceae	*Opuntia basilaris / chlorotica*	-0.08		-0.10		0.00		0.00	
Cactaceae	*Opuntia basilaris / echinocarpa*	-0.79		-0.73		0.00		0.00	
Cactaceae	*Opuntia basilaris / erinacea*	0.28		-0.28		0.00		0.00	
Cactaceae	*Opuntia basilaris / macrorhiza*	0.73		0.18		-0.98	-	-0.95	

		Beta Niche				Alpha Niche			
		Presence		Cover		Presence		Cover	
Family	**Congeneric Pair**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Cactaceae	*Opuntia basilaris / phaeacantha*	0.67		0.83		-0.51		-0.38	
Cactaceae	*Opuntia basilaris / polyacantha*	0.92		0.68		0.99	+	0.98	+
Cactaceae	*Opuntia basilaris / whipplei*	0.11		-0.33		0.00		0.00	
Cactaceae	*Opuntia chlorotica / echinocarpa*	-0.20		-0.20		0.00		0.00	
Cactaceae	*Opuntia chlorotica / erinacea*	0.14		0.75		0.00		0.00	
Cactaceae	*Opuntia chlorotica / macrorhiza*	0.08		-0.01		0.95	+	0.59	
Cactaceae	*Opuntia chlorotica / phaeacantha*	-0.10		-0.12		0.00		0.00	
Cactaceae	*Opuntia chlorotica / polyacantha*	-0.30		0.51		0.00		0.00	
Cactaceae	*Opuntia chlorotica / whipplei*	0.08		0.04		0.00		0.00	
Cactaceae	*Opuntia echinocarpa / erinacea*	-0.48		-0.48		0.87		0.87	
Cactaceae	*Opuntia echinocarpa / macrorhiza*	-0.47		0.31		-0.31		-0.31	
Cactaceae	*Opuntia echinocarpa / phaeacantha*	-0.53		-0.56		0.00		0.00	
Cactaceae	*Opuntia echinocarpa / polyacantha*	-0.17		-0.23		0.00		0.00	
Cactaceae	*Opuntia echinocarpa / whipplei*	-0.14		0.62		0.00		0.00	
Cactaceae	*Opuntia erinacea / macrorhiza*	0.04		-0.10		-0.63		-0.94	
Cactaceae	*Opuntia erinacea / phaeacantha*	0.31		-0.32		0.84		0.15	
Cactaceae	*Opuntia erinacea / polyacantha*	-0.04		0.76		0.00		0.00	
Cactaceae	*Opuntia erinacea / whipplei*	0.98	+	0.17		0.94		0.00	
Cactaceae	*Opuntia macrorhiza / phaeacantha*	0.35		0.20		-0.93		-0.93	
Cactaceae	*Opuntia macrorhiza / polyacantha*	1.00	+	0.87		-0.69		-0.69	
Cactaceae	*Opuntia macrorhiza / whipplei*	0.44		0.68		-0.01		0.99	+
Cactaceae	*Opuntia phaeacantha / polyacantha*	0.87		0.86		0.00		0.00	
Cactaceae	*Opuntia phaeacantha / whipplei*	0.76		0.40		0.99	+	0.95	+
Cactaceae	*Opuntia polyacantha / whipplei*	0.52		0.50		0.00		0.00	
Polemoniaceae	*Phlox austromontana / hoodii*	1.00	+	1.00	+	-0.18		-0.18	
Polemoniaceae	*Phlox austromontana / longifolia*	-0.80		-0.83		0.00		0.00	
Polemoniaceae	*Phlox austromontana / pulvinata*	0.99	+	0.99	+	0.00		0.00	
Polemoniaceae	*Phlox hoodii / longifolia*	0.00		0.00		0.00		0.00	
Polemoniaceae	*Phlox hoodii / pulvinata*	0.84		0.84		0.00		0.00	
Polemoniaceae	*Phlox longifolia / pulvinata*	0.00		0.00		0.00		0.00	
Polemoniaceae	*Ipomopsis aggregata / congesta*	-0.49		0.90		0.00		0.00	
Ericaceae	*Arctostaphylos patula / pungens*	0.44		-0.14		0.67		-0.44	
Lamiaceae	*Mentha arvensis / piperita*	0.00		0.00		0.00		0.00	
Orobanchaceae	*Castilleja chromosa / flava*	0.37		0.37		0.00		0.00	
Orobanchaceae	*Castilleja chromosa / linariifolia*	-0.38		-0.38		0.00		0.00	
Orobanchaceae	*Castilleja flava / linariifolia*	0.50		0.50		0.00		0.00	
Orobanchaceae	*Cordylanthus kingii / parviflorus*	-0.34		-0.18		0.00		0.00	
Plantaginaceae	*Penstemon caespitosus / eatonii*	0.41		0.93		0.30		0.30	
Plantaginaceae	*Penstemon caespitosus / higginsii*	-0.40		0.83		0.00		0.00	
Plantaginaceae	*Penstemon caespitosus / humilis*	0.30		0.91		0.00		0.00	
Plantaginaceae	*Penstemon caespitosus / lentus*	0.96	+	0.58		0.00		0.00	
Plantaginaceae	*Penstemon caespitosus / linarioides*	0.80		0.03		0.00		0.00	
Plantaginaceae	*Penstemon caespitosus / pachyphyllus*	-0.81		-0.81		0.00		0.00	
Plantaginaceae	*Penstemon caespitosus / palmeri*	0.69		-0.06		-0.13		-0.04	
Plantaginaceae	*Penstemon caespitosus / rostriflorus*	0.47		0.68		0.00		0.00	

		Beta Niche				Alpha Niche			
		Presence		Cover		Presence		Cover	
Family	**Congeneric Pair**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Plantaginaceae	*Penstemon eatonii / higginsii*	-0.62		0.58		0.00		0.00	
Plantaginaceae	*Penstemon eatonii / humilis*	-0.33		0.49		0.00		0.00	
Plantaginaceae	*Penstemon eatonii / lentus*	0.75		0.56		0.00		0.00	
Plantaginaceae	*Penstemon eatonii / linarioides*	0.16		-0.25		0.00		0.00	
Plantaginaceae	*Penstemon eatonii / pachyphyllus*	-0.89		-0.89		0.00		0.00	
Plantaginaceae	*Penstemon eatonii / palmeri*	-0.74		-0.72		0.86		0.89	
Plantaginaceae	*Penstemon eatonii / rostriflorus*	0.71		0.78		0.00		0.00	
Plantaginaceae	*Penstemon higginsii / humilis*	0.76		0.98	+	0.00		0.00	
Plantaginaceae	*Penstemon higginsii / lentus*	-0.19		-0.19		0.00		0.00	
Plantaginaceae	*Penstemon higginsii / linarioides*	-0.44		-0.81		0.00		0.00	
Plantaginaceae	*Penstemon higginsii / pachyphyllus*	-0.66		-0.66		0.00		0.00	
Plantaginaceae	*Penstemon higginsii / palmeri*	-0.99	-	-0.96	-	0.00		0.00	
Plantaginaceae	*Penstemon higginsii / rostriflorus*	0.60		0.68		0.00		0.00	
Plantaginaceae	*Penstemon humilis / lentus*	0.00		0.00		0.00		0.00	
Plantaginaceae	*Penstemon humilis / linarioides*	-0.37		-0.65		0.00		0.00	
Plantaginaceae	*Penstemon humilis / pachyphyllus*	-0.14		-0.14		0.00		0.00	
Plantaginaceae	*Penstemon humilis / palmeri*	-0.79		-0.72		0.00		0.00	
Plantaginaceae	*Penstemon humilis / rostriflorus*	0.75		0.75		0.00		0.00	
Plantaginaceae	*Penstemon lentus / linarioides*	0.85		0.86		0.00		0.00	
Plantaginaceae	*Penstemon lentus / pachyphyllus*	0.00		0.00		0.00		0.00	
Plantaginaceae	*Penstemon lentus / palmeri*	1.00	+	0.87		0.00		0.00	
Plantaginaceae	*Penstemon lentus / rostriflorus*	0.00		0.00		0.00		0.00	
Plantaginaceae	*Penstemon linarioides / pachyphyllus*	-0.40		0.45		0.00		0.00	
Plantaginaceae	*Penstemon linarioides / palmeri*	0.84		1.00	+	-0.07		0.00	
Plantaginaceae	*Penstemon linarioides / rostriflorus*	0.01		-0.32		0.00		0.00	
Plantaginaceae	*Penstemon pachyphyllus / palmeri*	-0.28		0.58		0.00		0.00	
Plantaginaceae	*Penstemon pachyphyllus / rostriflorus*	0.00		0.00		0.00		0.00	
Plantaginaceae	*Penstemon palmeri / rostriflorus*	-0.49		-0.36		0.00		0.00	
Oleaceae	*Fraxinus anomala / velutina*	-0.99	-	0.52		0.67		0.03	
Solanaceae	*Physalis hederifolia / heterophylla*	0.00		0.00		0.00		0.00	
Asteraceae	*Cirsium arizonicum / calcareum*	0.00		0.00		0.00		0.00	
Asteraceae	*Cirsium arizonicum / vulgare*	0.00		0.00		0.00		0.00	
Asteraceae	*Cirsium arizonicum / wheeleri*	0.10		0.76		0.00		0.00	
Asteraceae	*Cirsium calcareum / vulgare*	0.00		0.00		0.00		0.00	
Asteraceae	*Cirsium calcareum / wheeleri*	0.13		0.10		0.00		0.00	
Asteraceae	*Cirsium vulgare / wheeleri*	-0.11		-0.11		0.00		0.00	
Asteraceae	*Stephanomeria exigua / tenuifolia*	0.00		0.00		0.00		0.00	
Asteraceae	*Senecio eremophilus / integerrimus*	0.00		0.00		0.00		0.00	
Asteraceae	*Senecio eremophilus / multilobatus*	-0.91		-0.91		0.00		0.00	
Asteraceae	*Senecio eremophilus / spartioides*	-0.84		-0.89		0.00		0.00	
Asteraceae	*Senecio integerrimus / multilobatus*	-0.89		-0.89		0.00		0.00	
Asteraceae	*Senecio integerrimus / spartioides*	-0.36		0.10		0.00		0.00	
Asteraceae	*Senecio multilobatus / spartioides*	-1.00	-	-1.00	-	-0.32		-0.32	
Asteraceae	*Tetradymia axillaris / canescens*	0.42		0.79		0.00		0.00	

Family	Congeneric Pair	Beta Niche				Alpha Niche			
		Presence		Cover		Presence		Cover	
		Prob	Sig	Prob	Sig	Prob	Sig	Prob	Sig
Asteraceae	*Artemisia campestris / dracunculus*	0.44		0.76		-0.08		0.03	
Asteraceae	*Artemisia campestris / filifolia*	-0.99	-	-0.98	-	0.00		0.00	
Asteraceae	*Artemisia campestris / ludoviciana*	-0.41		0.08		-0.84		-0.83	
Asteraceae	*Artemisia campestris / nova*	-0.70		-0.92		0.31		-0.11	
Asteraceae	*Artemisia campestris / tridentata*	-0.29		-0.93		0.71		0.66	
Asteraceae	*Artemisia dracunculus / filifolia*	-0.92		-0.41		0.66		0.42	
Asteraceae	*Artemisia dracunculus / ludoviciana*	-0.42		-0.11		0.30		0.98	+
Asteraceae	*Artemisia dracunculus / nova*	-0.70		-0.93		-0.07		-0.02	
Asteraceae	*Artemisia dracunculus / tridentata*	-0.08		0.36		0.14		0.53	
Asteraceae	*Artemisia filifolia / ludoviciana*	-0.99	-	-0.96	-	-0.50		-0.33	
Asteraceae	*Artemisia filifolia / nova*	-1.00	-	-1.00	-	0.00		0.00	
Asteraceae	*Artemisia filifolia / tridentata*	-1.00	-	0.41		-0.98	-	-0.98	-
Asteraceae	*Artemisia ludoviciana / nova*	-0.85		-0.62		-0.11		-0.34	
Asteraceae	*Artemisia ludoviciana / tridentata*	-0.45		-0.95		-0.97	-	-0.98	-
Asteraceae	*Artemisia nova / tridentata*	-0.98	-	-1.00	-	-0.84		-0.92	
Asteraceae	*Erigeron argentatus / divergens*	0.00		0.00		0.00		0.00	
Asteraceae	*Erigeron argentatus / pumilus*	0.00		0.00		0.00		0.00	
Asteraceae	*Erigeron argentatus / speciosus*	0.00		0.00		0.00		0.00	
Asteraceae	*Erigeron argentatus / utahensis*	0.97	+	0.94		0.00		0.00	
Asteraceae	*Erigeron divergens / pumilus*	0.00		0.00		0.00		0.00	
Asteraceae	*Erigeron divergens / speciosus*	0.00		0.00		0.00		0.00	
Asteraceae	*Erigeron divergens / utahensis*	-0.08		-0.08		0.00		0.00	
Asteraceae	*Erigeron pumilus / speciosus*	0.51		0.40		0.00		0.00	
Asteraceae	*Erigeron pumilus / utahensis*	-0.25		-0.36		0.00		0.00	
Asteraceae	*Erigeron speciosus / utahensis*	-0.77		-0.77		0.00		0.00	
Asteraceae	*Haplopappus gracilis / canescens*	-0.36		-0.36		0.00		0.00	
Asteraceae	*Gutierrezia microcephala / sarothrae*	-0.32		0.94		-1.00	-	-1.00	-
Asteraceae	*Chrysothamnus depressus / viscidiflorus*	-0.11		0.08		0.00		0.00	
Asteraceae	*Chrysothamnus nauseosus / parryi*	0.60		0.87		0.31		0.35	
Asteraceae	*Chrysothamnus nauseosus / linearifolius*	-0.84		-0.98	-	0.00		0.00	
Asteraceae	*Chrysothamnus parryi / linearifolius*	0.00		0.00		0.00		0.00	
Asteraceae	*Chaenactis douglasii / stevioides*	-0.32		-0.32		0.00		0.00	
Asteraceae	*Brickellia atractyloides / californica*	-0.39		-0.39		0.00		0.00	
Asteraceae	*Brickellia atractyloides / grandiflora*	-0.53		-0.67		0.00		0.00	
Asteraceae	*Brickellia atractyloides / longifolia*	0.23		-0.65		0.00		0.00	
Asteraceae	*Brickellia atractyloides / microphylla*	0.81		0.38		0.00		0.00	
Asteraceae	*Brickellia californica / grandiflora*	0.44		0.75		0.00		0.00	
Asteraceae	*Brickellia californica / longifolia*	-0.58		-0.50		0.00		0.00	
Asteraceae	*Brickellia californica / microphylla*	-0.21		0.00		0.00		0.00	
Asteraceae	*Brickellia grandiflora / longifolia*	-0.92		-0.92		0.00		0.00	
Asteraceae	*Brickellia grandiflora / microphylla*	-0.27		0.00		0.00		0.00	
Asteraceae	*Brickellia longifolia / microphylla*	0.94		0.98	+	0.00		0.00	
Apiaceae	*Osmorhiza depauperata / occidentalis*	0.39		0.77		0.00		0.00	
Caprifoliaceae	*Symphoricarpos longiflorus / oreophilus*	-0.84		-0.80		0.00		0.00	

[1] Cover-based overlap could not be calculated for *Salix scouleriana* because it lacked cover values in the dataset used for this analysis

APPENDIX 3.3

Results of niche overlap significance tests comparing phylogenetic sister groups (genus and above) for vascular plants recorded in the USGS-NPS vegetation characterization of Zion National Park, Utah (Cogan et al. 2004). Null model distributions of beta niche overlap (across habitats) and alpha niche overlap (across plots within habitats), using both presence and cover measures, were built through randomization and compared with observed overlap values. Prob=probabilities ranging from -1 (more segregated than expected) to 1 (more aggregated than expected). Sig=cases of statistically significant segregation (-) or aggregation (+), i.e. $p \leq 0.05$ for a two-tailed test. Note: This nested sequence of sister groups follows the phylogenetic trees in Fig. 1 and 3-6; sister groups comprised of additive or subtractive combinations of taxa are separated by a slash.

	Beta Niche				**Alpha Niche**			
	Presence		**Cover**		**Presence**		**Cover**	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Moniliformopses / Spermatophyta	-1.00	-	-1.00	-	0.00		-0.29	
Equisetum / Filicales	-0.89		-0.96	-	0.13		0.46	
Pteridium / Eupolypods	0.08		0.30		0.00		0.00	
Asplenium / *Polypodium*	0.00		0.00		0.00		0.00	
Gymnosperms / Magnoliophyta	-1.00	-	-1.00	-	0.00		-1.00	-
Coniferales / *Ephedra*	-1.00	-	-0.98	-	0.87		0.67	
Cupressaceae / Pinaceae	-0.99	-	-1.00	-	1.00	+	0.99	+
Cupressus / *Juniperus*	-0.73		-0.83		0.00		0.00	
Abies / *Pinus* + *Pseudotsuga*	-1.00	-	-1.00	-	0.03		0.65	
Pinus / *Pseudotsuga*	-1.00	-	-1.00	-	-0.20		0.37	
Liliopsida / eudicots	-0.95	-	-1.00	-	0.00		-0.16	
commelinids + Asparagales / *Calochortus*	0.34		0.18		0.00		-0.03	
commelinids / Asparagales	-0.96	-	-0.67		-0.95	-	-0.71	
Tradescantia / Poales	-0.05		0.01		0.13		0.30	
Typha / Cyperaceae + Juncaceae + Poaceae	-0.88		-0.17		0.00		0.87	
Cyperaceae + Juncaceae / Poaceae	-1.00	-	-1.00	-	-0.17		0.43	
Cyperaceae / Juncaceae	-1.00	-	0.99	+	0.95	+	0.97	+
Carex + *Scirpus* / *Eleocharis*	0.16		1.00	+	0.58		0.94	
Carex / *Scirpus*	-0.76		1.00	+	0.22		0.87	
Juncus / *Luzula*	1.00	+	1.00	+	0.65		0.70	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Poaceae (identified to genus) / Poaceae (not identified to genus)	-0.75		0.32		0.00		0.69	
Aristidoideae + Arundinoideae + Chloridoideae + Panicoideae / Pooideae	-1.00	-	-0.82		0.95		-0.09	
Aristidoideae + Arundinoideae + Chloridoideae / Panicoideae	-0.94		-0.30		0.62		0.88	
Aristida / Arundinoideae + Chloridoideae	-0.67		0.08		0.99	+	-0.04	
Phragmites / Cynodonteae	0.09		-0.01		0.00		0.00	
Muhlenbergia + *Hilaria* + *Bouteloua* + *Erioneuron* / *Sporobolus* + *Distichlis*	-0.90		0.22		0.44		0.80	
Muhlenbergia + *Hilaria* + *Bouteloua* / *Erioneuron*	0.05		0.10		0.00		-0.15	
Muhlenbergia + *Hilaria* / *Bouteloua*	-1.00	-	-0.83		-0.09		0.38	
Muhlenbergia / *Hilaria*	-0.99	-	-0.95	-	-0.88		-0.88	
Sporobolus / *Distichlis*	0.17		0.09		0.00		0.00	
Andropogoneae / *Cenchrus*	0.00		0.00		0.00		0.00	
Andropogon + *Schizachyrium* / *Sorghastrum*	0.94		0.94		0.00		0.00	
Andropogon / *Schizachyrium*	0.00		0.00		0.00		0.00	
Stipeae / Poeae + Aveneae + Bromeae + Triticeae	-0.79		-0.98	-	-0.37		0.18	
Stipeae (identified to genus) / Stipeae (not identified to genus)	0.58		0.94		0.26		0.55	
Achnatherum + *Nassella* / *Hesperostipa*	-0.87		0.99	+	0.03		0.84	
Achnatherum / *Nassella*	-1.00	-	-0.98	-	0.41		0.84	
Poeae + Aveneae / Bromeae + Triticeae	-1.00	-	-0.70		-0.77		0.75	
Poeae / Aveneae	-0.98	-	-0.99	-	0.86		0.33	
Phleum + *Poa* + *Puccinellia* / *Dactylis* + *Festuca*	0.44		0.75		0.14		0.26	
Phleum + *Poa* / *Puccinellia*	-0.04		0.10		0.00		0.86	
Phleum / *Poa*	-0.02		0.15		0.00		0.78	
Dactylis / *Festuca*	-0.63		-0.56		0.00		0.00	
Agrostis + *Polypogon* + *Calamagrostis* / *Koeleria*	-0.95		-0.98	-	0.00		0.00	
Agrostis + *Polypogon* / *Calamagrostis*	-0.41		-0.41		0.00		0.00	
Agrostis / *Polypogon*	-0.37		-0.37		0.00		0.00	
Bromus / Triticeae	-0.99	-	-0.83		0.70		0.21	
Hordeum + *Agropyron* / *Elymus*	0.58		0.65		0.65		0.04	
Hordeum / *Agropyron*	0.00		0.00		0.00		0.00	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Sisyrinchium / Alliaceae + Ruscaceae + Agavaceae	-0.08		-0.24		0.61		0.78	
Allium / Ruscaceae + Agavaceae	-0.67		-0.98	-	-0.15		-0.17	
Maianthemum / *Yucca*	-1.00	-	-1.00	-	0.23		0.09	
Ranunculales / core eudicots	-1.00	-	-1.00	-	0.00		1.00	+
Mahonia / Ranunculaceae	-1.00	-	-0.35		-0.11		0.92	
Clematis / *Aquilegia* + *Thalictrum*	0.33		0.80		0.81		0.47	
Aquilegia / *Thalictrum*	0.33		-0.26		0.00		0.00	
rosids + Saxifragales / Santalales + Caryophyllales + asterids	-0.82		-1.00	-	0.47		-1.00	-
rosids / *Heuchera*	-1.00	-	-0.96	-	0.00		0.22	
rosids - Vitales / *Vitis*	-0.65		0.43		0.00		0.90	
fabids / malvids	-1.00	-	-1.00	-	0.95	+	0.93	
fabids - Zygophyllales / Zygophyllales	0.41		-0.01		0.00		-0.25	
Fagales + Rosales + Fabales / Celastrales + Malpighiales	-1.00	-	-1.00	-	0.05		-0.47	
Fagales + Rosales / Fabaceae	-1.00	-	-1.00	-	-0.06		0.83	
Fagales / Rosales	-0.76		-0.95	-	1.00	+	0.55	
Betula / *Quercus*	-1.00	-	-1.00	-	0.54		-0.42	
Rosaceae / Elaeagnaceae + Rhamnaceae + Ulmaceae	-0.81		-0.94		0.39		-0.31	
Dryadoideae / Rosoideae + Spiraeoideae	-0.92		-0.58		0.91		1.00	+
Cercocarpus / *Purshia*	-0.60		0.65		0.64		-0.26	
Potentilleae / Spiraeoideae	-1.00	-	-0.01		0.58		-0.92	
Ivesia + *Potentilla* / *Rosa*	-0.51		0.36		0.00		0.00	
Ivesia / *Potentilla*	0.00		0.00		0.00		0.00	
Pyreae + Spiraeeae + Kerreae / *Prunus*	-1.00	-	-1.00	-	-0.08		0.68	
Pyreae + Spiraeeae / *Coleogyne*	-1.00	-	-1.00	-	-0.11		-0.36	
Pyreae / Spiraeeae	-0.26		-0.42		-0.28		0.64	
Amelanchier / *Peraphyllum*	-0.38		0.95	+	-0.11		0.09	
Holodiscus / *Petrophytum*	-0.14		-0.14		0.42		0.42	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	Prob	Sig	Prob	Sig	Prob	Sig	Prob	Sig
Elaeagnaceae + Rhamnaceae / *Celtis*	-0.91		-0.76		0.53		0.87	
Elaeagnaceae / *Ceanothus*	-1.00	-	-1.00	-	0.00		0.00	
Elaeagnus / *Shepherdia*	-0.99	-	-0.87		0.00		0.00	
Fabaceae (identified to genus) / Fabaceae (not identified to genus)	-0.49		-0.63		0.00		-0.11	
Prosopis / Papilionoideae	0.10		0.22		0.00		0.26	
Genisteae + Thermopsideae / Amorpheae + Psoraleeae + Hologalegina	-1.00	-	-0.82		0.96	+	0.98	+
Lupinus / *Thermopsis*	0.20		0.39		0.00		0.00	
Amorpheae / Psoraleeae + Hologalegina	-1.00	-	-1.00	-	0.62		-0.08	
Dalea / *Psorothamnus*	0.18		-0.16		0.00		0.00	
Psoralidium / Hologalegina	-0.03		-0.35		0.29		0.56	
Lotus / Galegeae + Trifolieae + Fabeae	-0.98	-	-0.95	-	0.98	+	0.34	
Galegeae / Trifolieae + Fabeae	-0.79		-0.56		-0.46		-0.28	
Astragalus / *Oxytropis*	-0.75		-0.80		0.00		0.00	
Trifolieae clade 1 / Trifolieae clade 2 + Fabeae	-1.00	-	-1.00	-	-0.08		-0.63	
Medicago / *Melilotus*	1.00	+	1.00	+	0.13		0.13	
Trifolium / Fabeae	-0.99	-	-0.98	-	0.28		0.70	
Lathyrus / *Vicia*	-0.97	-	-0.94		0.56		0.54	
Pachystima / Malpighiales	-1.00	-	-1.00	-	0.88		0.14	
Euphorbiaceae + Linaceae / Salicaceae + Violaceae	-1.00	-	-1.00	-	0.23		-0.40	
Euphorbiaceae / *Linum*	0.06		-0.03		-0.13		-0.13	
Tragia / Euphorbieae	0.16		0.11		0.00		0.00	
Chamaesyce / *Euphorbia*	-0.76		-0.80		-0.44		-0.44	
Salicaceae / *Viola*	-0.93		-0.99	-	0.00		0.00	
Populus / *Salix*	0.92		0.86		0.96	+	-0.09	
Tribulus / *Krameria*	0.00		0.00		0.00		0.00	
Brassicales + Malvales + Sapindales / Geraniales + Myrtales	-0.96	-	-1.00	-	0.04		-0.12	
Brassicales + Malvales / Sapindales	-1.00	-	-1.00	-	-0.53		0.25	
Brassicaceae / *Sphaeralcea*	-0.62		-0.19		0.16		-0.26	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Brassicaceae (identified to genus) / Brassicaceae (not identified to genus)	-0.94		-0.83		0.25		0.73	
Arabideae + Sisymbrieae + Schizopetaleae + Cardamineae + Lepidieae + Descurainieae + Physarieae / *Erysimum*	0.13		-0.29		0.68		0.75	
Arabideae + Sisymbrieae + Schizopetaleae + Cardamineae + Lepidieae + Descurainieae / *Physaria*	0.26		-0.19		-0.14		-0.23	
Arabideae + Sisymbrieae + Schizopetaleae + Cardamineae / Lepidieae + Descurainieae	-0.64		-0.62		-0.13		-0.13	
Arabideae + Sisymbrieae + Schizopetaleae / *Nasturtium*	-0.23		0.09		0.00		0.00	
Arabideae / Sisymbrieae + Schizopetaleae	-0.78		-0.97	-	-0.13		-0.13	
Arabis / *Draba*	1.00	+	1.00	+	-0.04		-0.04	
Sisymbrium / Schizopetaleae	-0.77		-0.38		0.00		0.00	
Streptanthus / *Stanleya*	-0.35		-0.35		0.00		0.00	
Lepidium / *Descurainia*	-0.30		-0.30		0.00		0.00	
Anacardiaceae / *Acer*	-1.00	-	-1.00	-	-0.07		-0.47	
Rhus / *Toxicodendron*	0.80		0.84		0.00		0.00	
Geraniaceae / Onagraceae	-0.92		-0.93		0.18		0.18	
Erodium / *Geranium*	-0.56		-0.56		0.00		0.00	
Epilobium / Onagreae	-0.72		-0.72		0.00		0.00	
Gayophytum / *Oenothera*	-0.64		-0.64		0.00		0.00	
Santalaceae / Caryophyllales + asterids	-0.94		0.25		0.09		0.95	
Phoradendron / *Comandra*	-0.16		-0.28		0.25		0.27	
Caryophyllales / asterids	-1.00	-	-1.00	-	0.82		0.54	
Polygonaceae + Tamaricaceae / Amaranthaceae + Caryophyllaceae + Nyctaginaceae + Cactaceae + Portulacaceae	-1.00	-	-0.96	-	0.98	+	1.00	+
Polygonaceae / *Tamarix*	-1.00	-	-1.00	-	0.38		0.71	
Eriogonum / Polygonoideae	-0.95	-	-0.96	-	0.79		0.74	
Polygonum / *Rumex*	-0.97	-	-0.97	-	0.00		0.00	
Amaranthaceae + Caryophyllaceae / Nyctaginaceae + Cactaceae + Portulacaceae	-1.00	-	-0.28		0.97	+	0.96	+
Amaranthaceae / Caryophyllaceae	-1.00	-	-1.00	-	0.22		-0.24	
Atriplex + *Chenopodium* + *Grayia* / *Salsola*	0.10		0.41		0.00		0.00	
Atriplex + *Chenopodium* / *Grayia*	0.83		0.85		0.39		-0.08	
Atriplex / *Chenopodium*	-0.97	-	-0.99	-	0.38		0.13	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Arenaria + *Stellaria* / Caryophyllaceae (not identified to genus)	-0.87		-0.52		0.00		0.00	
Arenaria / *Stellaria*	-0.83		-0.79		0.00		0.00	
Nyctaginaceae / Cactaceae + Portulacaceae	-0.97	-	-0.82		0.90		0.72	
Abronia / *Allionia* + *Mirabilis*	-0.58		-0.58		0.00		0.00	
Allionia / *Mirabilis*	0.99	+	0.99	+	0.66		0.66	
Cactaceae / *Claytonia*	-1.00	-	-1.00	-	-0.01		-0.01	
Echinocereus / *Opuntia*	-0.98	-	-1.00	-	0.98	+	0.68	
Fendlerella / asterids - Cornales	-0.32		-0.66		0.00		-0.66	
Ericales / lamiids + campanulids	-1.00	-	-1.00	-	-0.84		-1.00	-
Polemonioideae / Ericaceae	0.95		0.40		0.99	+	0.09	
Phlocideae / Gilieae + Loeselieae	-0.46		0.83		-0.19		-0.03	
Phlox + *Leptosiphon* / *Linanthus*	-0.79		-0.85		0.00		0.00	
Phlox / *Leptosiphon*	0.77		0.75		0.00		0.00	
Gilia / *Ipomopsis*	0.97	+	0.89		0.00		0.00	
Arctostaphylos / Monotropoideae	-0.84		-0.95	-	-0.10		0.43	
Pterospora / *Chimaphila*	0.00		0.00		0.00		0.00	
lamiids / campanulids	-0.52		-0.96	-	0.97	+	0.46	
Lamiales + Solanales + Gentianales / Boraginaceae	-0.25		0.84		0.58		-0.23	
Lamiales + Solanales / Gentianales	-0.99	-	-0.95		0.65		0.67	
Lamiales / Solanales	-0.99	-	0.13		0.05		0.88	
Lamiaceae + Orobanchaceae + Verbenaceae + Scrophulariaceae + Plantaginaceae / *Fraxinus*	-0.83		-1.00	-	0.27		-0.47	
Lamiaceae + Orobanchaceae + Verbenaceae + Scrophulariaceae / Plantaginaceae	-0.88		-0.93		0.53		0.97	+
Lamiaceae + Orobanchaceae + Verbenaceae / *Verbascum*	-0.76		-0.68		0.61		0.81	
Lamiaceae + Orobanchaceae / *Verbena*	-0.34		-0.58		0.00		0.00	
Mentheae / Rhinantheae	0.02		0.44		-0.28		-0.22	
Agastache + *Dracocephalum* + *Mentha* + *Monardella* / *Salvia*	-0.98	-	-0.96	-	0.00		0.00	
Agastache + *Dracocephalum* / *Mentha* + *Monardella*	-0.84		-0.84		0.00		0.00	
Agastache / *Dracocephalum*	0.00		0.00		0.00		0.00	
Mentha / *Monardella*	0.00		0.00		0.00		0.00	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Castilleja / *Cordylanthus*	-0.25		-0.45		0.86		0.82	
Antirrhineae + Plantagineae / Cheloneae	-0.98	-	-0.97	-	-0.06		-0.05	
Linaria / *Plantago*	-0.11		-0.11		0.00		0.00	
Collinsia / *Penstemon*	-0.51		-0.69		0.23		0.26	
Convolvulaceae / Solanaceae	0.50		0.36		0.24		0.76	
Convolvulus / *Ipomoea*	0.84		0.89		0.00		0.00	
Nicotiana / Solanoideae	0.17		0.10		0.00		0.00	
Physaleae + Solaneae + Datureae / *Lycium*	-0.97	-	-0.85		0.59		0.67	
Physaleae + Solaneae / *Datura*	-0.16		-0.16		0.71		0.71	
Physalis / *Solanum*	0.00		0.00		0.00		0.00	
Apocynaceae + Gentianaceae / Rubioideae	0.22		-0.64		0.00		0.00	
Apocynaceae / *Swertia*	0.36		0.21		0.00		0.00	
Apocynum / *Asclepias*	0.00		0.00		0.00		0.00	
Kelloggia / *Galium*	0.32		-0.60		0.00		0.00	
Boraginaceae (identified to genus) / Boraginaceae (not identified to genus)	0.09		-0.19		0.00		0.00	
Boraginoideae / Hydrophylloideae	-0.85		0.52		-0.92		-0.92	
Cryptantha + *Plagiobothrys* / *Mertensia*	-0.99	-	-0.97	-	0.00		0.00	
Cryptantha / *Plagiobothrys*	-0.42		-0.51		0.00		0.00	
Hydrophyllum / *Phacelia*	-0.78		-0.83		0.00		0.00	
Asteraceae / Apiales + Dipsacales	-1.00	-	-1.00	-	-0.84		-1.00	-
Asteraceae (identified to genus) / Asteraceae (not identified to genus)	-0.45		-0.71		0.18		0.53	
Cirsium / Cichorioideae + Asteroideae	-0.90		-0.60		0.47		-0.20	
Chicorieae / Asteroideae	-1.00	-	-0.99	-	0.92		0.64	
Agoseris + *Stephanomeria* + *Lygodesmia* + *Crepis* + *Taraxacum* + *Hypochaeris* + *Lactuca* / *Tragopogon*	-0.78		-0.27		-0.04		-0.14	
Agoseris + *Stephanomeria* + *Lygodesmia* / *Crepis* + *Taraxacum* + *Hypochaeris* + *Lactuca*	-0.65		-0.48		0.00		0.00	
Agoseris + *Stephanomeria* / *Lygodesmia*	0.84		0.58		0.00		0.00	
Agoseris / *Stephanomeria*	0.41		0.42		0.00		0.00	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Crepis + *Taraxacum* + *Hypochaeris* / *Lactuca*	0.32		0.32		0.82		0.82	
Crepis + *Taraxacum* / *Hypochaeris*	-0.18		-0.18		0.00		0.00	
Crepis / *Taraxacum*	0.52		0.52		0.00		0.00	
Senecioneae / Asteroideae - Senecioneae	-0.87		0.93		0.81		-0.26	
Senecio / *Tetradymia*	-0.85		-0.90		0.36		0.46	
Anthemideae + Astereae + Gnaphalieae / Plucheeae + Helenieae + Bahieae + Chaenactideae + Eupatorieae + Perityleae + Madieae + Heliantheae	-0.96	-	-0.76		0.94		-0.53	
Anthemideae + Astereae / *Antennaria*	-0.83		-0.84		0.79		0.85	
Anthemideae / Astereae	-0.72		-1.00	-	0.99	+	0.43	
Achillea / *Artemisia* + *Sphaeromeria*	-1.00	-	-1.00	-	0.29		-0.96	-
Artemisia / *Sphaeromeria*	-0.07		-0.07		-0.16		0.35	
Baccharis / Astereae - *Baccharis*	-1.00	-	-0.99	-	0.50		0.55	
Erigeron + *Chrysopsis* + *Chaetopappa* + *Townsendia* + *Symphyotrichum* + *Eurybia* + *Machaeranthera* + *Gutierrezia* / *Solidago* + *Petradoria* + *Chrysothamnus* + *Hesperadoria* + *Ericameria*	-0.72		-1.00	-	-0.26		-0.71	
Erigeron + *Chrysopsis* + *Chaetopappa* + *Townsendia* + *Symphyotrichum* + *Eurybia* + *Machaeranthera* / *Gutierrezia*	-1.00	-	-1.00	-	-0.60		-0.95	-
Erigeron + *Chrysopsis* + *Chaetopappa* + *Townsendia* / *Symphyotrichum* + *Eurybia* + *Machaeranthera*	0.21		0.08		0.77		0.93	
Erigeron + *Chrysopsis* + *Chaetopappa* / *Townsendia*	0.79		-0.12		0.80		0.52	
Erigeron + *Chrysopsis* / *Chaetopappa*	-0.40		0.17		0.26		0.81	
Erigeron / *Chrysopsis*	-0.90		-0.56		0.93		0.73	
Asterinae spp. + *Symphyotrichum* / *Eurybia* + *Machaeranthera*	0.59		0.13		-0.23		0.37	
Asterinae spp. / *Symphyotrichum*	-0.24		-0.24		0.00		0.00	
Eurybia / *Machaeranthera*	-0.22		-0.22		0.00		0.00	
Solidago + *Petradoria* + *Chrysothamnus* + *Hesperodoria* / *Ericameria*	-0.96	-	0.05		-0.02		-0.06	
Solidago + *Petradoria* / *Chrysothamnus* + *Hesperodoria*	-0.98	-	-0.78		0.00		0.66	
Solidago / *Petradoria*	0.97	+	1.00	+	0.00		0.00	
Chrysothamnus / *Hesperodoria*	-0.71		-0.39		0.00		0.00	

	Beta Niche				Alpha Niche			
	Presence		Cover		Presence		Cover	
Sister Group Pair	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**	**Prob**	**Sig**
Pluchea / Helenieae + Bahieae + Chaenactideae + Eupatorieae + Madieae + Heliantheae	-0.90		0.91		0.00		0.00	
Helenieae / Bahieae + Chaenactideae + Eupatorieae + Madieae + Heliantheae	0.07		-0.31		0.00		0.00	
Baileya / Gaillardia	0.00		0.00		0.00		0.00	
Bahieae + Chaenactideae / Eupatorieae + Madieae + Heliantheae	-0.41		-0.95	-	-0.59		-0.93	
Hymenopappus / Chaenactis	0.02		0.02		-0.36		-0.36	
Eupatorieae + Madieae / Heliantheae	-0.77		-0.90		-0.76		-0.67	
Brickellia / Arnica	-0.03		-0.23		0.00		0.00	
Ambrosia + Helianthus + Viguiera + Geraea + Balsamorhiza + Wyethia / Helianthella	-0.03		-0.48		0.82		0.96	+
Ambrosia + Helianthus + Viguiera + Geraea / Balsamorhiza + Wyethia	0.40		0.91		0.00		0.00	
Ambrosia / Helianthus + Viguiera + Geraea	-0.46		-0.46		0.00		0.00	
Helianthus + Viguiera / Geraea	-0.43		-0.43		0.00		0.00	
Helianthus / Viguiera	-0.34		-0.34		0.00		0.00	
Balsamorhiza / Wyethia	0.98	+	0.43		0.79		0.81	
Apiaceae / Dipsacales	-0.75		0.36		0.95		0.86	
Lomatium / Osmorhiza	0.94		0.85		0.28		0.61	
Sambucus / Symphoricarpos	-0.76		-0.86		0.00		0.00	