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Factors Determining Alpine Species Distribution on Goliath Peak, Front Range, Colorado, U.S.A.

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Abstract

The effect of environmental factors on the distribution of alpine plant community types has been extensively studied in Colorado. Much less attention has been paid to the effects of these factors within community types, however. Transects were placed in the alpine zone of Goliath Peak in the Front Range of the Colorado Rocky Mountains. Species presences were tallied in 1-m² rectangular plots. Fuzzy set ordination (FSO) was used to determine which environmental factors were responsible for changes in species composition. Most sites fell into the fellfield or dry meadow community types. Water availability, as indicated by elevation, estimated winter snow depth and, less strongly, soil texture, was a strong factor associated with changes in plant community composition, both within and among community types. Temperature, as indicated by aspect, was also associated with these changes. The lack of *Kobresia myosuroides* at Goliath Peak appears to be caused by snow depths too deep or too shallow for this species. FSO proved to be more effective when environmental factors were ordinated separately rather than sequentially, as originally suggested. This was confirmed by a Bray-Curtis ordination. A species-site biplot showed how species and sites can be displayed together on the same fuzzy set ordination.

Introduction

Alpine areas in the Rocky Mountains have been extensively studied, particularly at Niwot Ridge and surrounding areas in Colorado (Komárková and Webber, 1978; Komárková, 1979, 1980; May and Webber, 1982; Eddleman and Ward, 1984; Isard, 1986; Walker et al., 1993; Walker et al., 1994, 2001). Several of these studies have found that snow cover and soil moisture, which are influenced by wind and topographic patterns, are the most important factors that determine the distribution of plant communities (e.g., Komárková and Webber, 1978; May and Webber, 1982; Isard, 1986; Walker et al., 1993; Walker et al., 2001). Indeed, the occurrence of many of these communities is determined by what has been referred to as “mesotopographic” features (Billings, 1998). For example, the dry fellfield communities at Niwot Ridge occur on dry, wind-swept ridges that are generally snow free during the winter, with a relatively long growing season. However, comparatively little attention has been paid to factors that influence species composition within these communities. Species diversity is relatively high in these alpine communities, and the number of species found within each community is both high and variable. Other factors may be responsible for species turnover within these communities. For example, the distribution of vegetation units at Niwot Ridge was influenced by both altitude and distance from the continental divide combined (Komárková and Webber, 1978). It is possible, however, that factors such as elevation or aspect might explain species turnover within a particular vegetation unit, e.g., the dry fellfield community type.

Alpine vegetation has been analyzed primarily with classification and ordination techniques. In the latter case, indirect gradient analyses have usually been used. These kinds of ordination methods are useful when little is known about the factors that influence vegetation distribution. They are a class of exploratory data techniques that are

useful in describing a site, but they cannot be used to test hypotheses regarding the role of environmental factors in determining species distributions (Gauch, 1982). For that purpose, direct gradient analyses are appropriate (Palmer, 1993). However, many direct gradient techniques assume a linear relationship between environmental factors (or linear combinations of these factors) and species response, even though community composition does not always respond linearly to environmental factors [ter Braak, 1986].

Fuzzy set ordination (FSO; Roberts, 1986) is a direct gradient analysis technique that does not require that there be linear relationships among environmental factors and patterns of community change. Thus, it offers an alternative to some of the techniques now commonly used. The advantages and disadvantages of FSO are not as well known as the strengths and shortcomings of other techniques, although Boyce and Ellison (2001) evaluated its performance with presence/absence data. However, FSO is the direct gradient analysis counterpart of Bray-Curtis (polar) ordination (Bray and Curtis, 1957). Thus, the relationships found by FSO should also be reflected in a Bray-Curtis ordination performed after the FSO.

Our knowledge of alpine plant communities in Colorado is based primarily on Niwot Ridge and the nearby Indian Peaks area. It would be useful to examine other areas to see how universal these patterns are in other areas of Colorado. Plant species on Goliath Peak, which is located on the Mount Evans massif about 50 km south of Niwot Ridge, were inventoried by Hartman and Mitchell (1979), but factors responsible for species distribution were not examined in that study. Part of the alpine area on Goliath Peak, i.e., the eastern part of the “saddle,” is located in the Mount Goliath Research Natural Area, created to preserve a large stand of bristlecone pine (*Pinus aristata* Bailey) which has been the subject of several studies (Krebs, 1972, 1973; Brunstein and Yamaguchi, 1992; Schoettle, 1994; Ranne et al., 1997; Schauer,

1999; Schauer et al., 2001). The Pesman Trail, which runs along the eastern side of Goliath Peak, is maintained by the Denver Botanic Gardens, and some of the data collected by Gardens staff for inventory purposes from the alpine area of the eastern saddle, as well as the nearby subalpine, were presented in Boyce and Ellison (2001). That study noted a strong elevational gradient in species composition, although the gradient included treeline sites as well as alpine sites. Another interesting feature of the Goliath Peak area noted by Hartman and Mitchell (1979) was the lack of *Kobresia myosuroides*, a sedge that is one of the most important species found at Niwot Ridge, particularly in the Saddle research area (Walker et al., 2001). The objective of the present study is to determine the factors responsible for species distributions in the saddle area of Goliath Peak. We also demonstrate the utility of FSO for these kinds of data and extend the manner in which the findings of this ordination technique may be interpreted. Finally, as FSO is still a relatively new technique, we test our findings against those found with Bray-Curtis ordination.

Materials and Methods

This study was carried out on Goliath Peak (39°38'N, 105°36'W, 3723 m elevation), a subsidiary peak of the Mount Evans massif, about 50 km west of Denver. The transects were laid on both sides of a saddle in the alpine zone. They were laid from a road that runs across the top of the saddle between Goliath Peak and the rest of the massif. One side of the saddle faced roughly northeast (~50°; hereafter referred to as the east exposure), whereas the other faced roughly northwest (~305°; hereafter referred to as the west exposure). A central transect was laid, beginning 50 m from the edge of the road (~3700 m) and proceeding downhill to treeline (~3560 m). Every 50 m, one plot was established. Plots were also established 50 m to either side of the central transect, perpendicular to its direction. A short piece of steel reinforcing bar was placed to mark the upper left-hand corner of the plot, and a numbered aluminum tag was tied to it with wire. A rectangular 1.0 m² (0.7 m × 1.4 m) frame, constructed of PVC piping, was laid on the ground with the long axis parallel to the slope to delineate the plot. Total transect distance was 500 m on the east exposure and 550 m on the west exposure.

At each plot, elevation, slope, and aspect were measured and recorded. Aspect was converted to an aspect value (AV), where $AV = [\cos(\text{aspect}^\circ - 45^\circ) + 1]/2$, so that northeast aspects would have a value near 1 and those with southwest aspects would have a value near 0. Slope and aspect were used to calculate a dimensionless heat load (HL), using equation (3) of McCune and Keon (2002). Within each plot, the presence of all species was recorded. Species were usually identified in the field. If an identification could not be made, a specimen was collected for identification at the Denver Botanic Gardens. A soil sample, consisting of the top 5 cm, was also collected from the center of the plot. Soil pH was determined from a small portion of this sample.

Soils were then dried at 105°C to constant weight. After sieving to remove soil fractions greater than 2 mm in diameter, a subsample was removed and ground to a fine power in a ball mill (Cianflone 2601). Total carbon and nitrogen concentration was obtained from an element analyzer (LECO CHN-1000). The remainder of the soil was separated into sand and silt + clay fractions using the hydrometer method (Lewis and McConchie, 1994). Visible pieces of organic matter were first removed with tweezers, followed by treatment with 30% hydrogen peroxide. Samples were then shaken for 12 h with sodium hexametaphosphate as a dispersant to prevent clay particles from forming aggregates, after which hydrometer reading were taken. Soil texture was expressed as the percentage of sand + silt + clay that was silt + clay.

Snow depth at each site was estimated by using the optimal snow depth classes reported for the 50 most common species on the Niwot Ridge Saddle area (Walker et al., 1993). For each of these species, the

midpoint of each snow depth class was computed. Then for each plot, a median snow depth was computed from these midpoints. Some of these species are found under many different snow depths (Walker et al., 1993); these species were not included in these estimates. A median depth was used rather than a mean depth, as the former is less sensitive to outliers than the latter.

Data were first subjected to Spearman rank correlation to find factors that were correlated with each other. A Spearman r implies only a monotonic relationship between factors, rather than a linear one suggested by a significant Pearson r (Zar, 1984); as ecological relationships are often nonlinear (Beals, 1984), we therefore made use of rank correlations throughout this study. Data were then analyzed with fuzzy set ordination (FSO; Roberts, 1986; Boyce, 1998; Boyce and Ellison, 2001) to find environmental factors that were responsible for vegetation patterns. As species presence was strongly affected by elevation (see Results), we expected elevation to have an important effect on community composition. Other factors that were not correlated with elevation or with each other were also incorporated into the ordination. Although snow depth was correlated with elevation, we also included it in the ordination, as we expected it to be important.

FSO was introduced by Roberts (1986) as an alternative to traditional direct gradient analysis ordination techniques. As in other direct gradient analysis methods, the investigator hypothesizes a relationship between the environment and the vegetation before performing the ordination. Samples are assigned memberships in sets that can range from 0 to 1, e.g., the values of a fuzzy set of sample site elevations would range from 0 (the lowest) to 1 (the highest). FSO employs an operation known as the anticommutative difference (Roberts, 1986, 1987), which can be understood as “while not.” This can be used, for example, to construct a fuzzy set that includes the membership of sites that are similar in composition to high elevation sites while not actually at high elevation, or apparent elevation. First, the set of high-elevation plots μ_A is constructed, where the lowest elevation plot has a membership of 0, the highest elevation plot has a membership of 1, and other plots have intermediate values that are essentially elevations normalized between 0 and 1. The set of low-elevation plots μ_B is then calculated, such that for plot x , $\mu_B(x) = 1 - \mu_A(x)$. Thus, for the highest plot $x = h$, $\mu_A(h) = 1$ and for the lowest plot, $\mu_B(l) = 0$. Then, a set of plots similar to high elevation plots is calculated as:

$$\mu_C(x) = \frac{\sum_{y \neq x} [S_{xy}(\mu_A(y))]}{\sum_{y \neq x} [\mu_A(y)]} \quad (1)$$

where S_{xy} is the similarity between plots x and y , $\mu_A(y)$ is the membership of plot y in the set of high elevation plots, and $\mu_C(x)$ is the membership of plot x in the set of plots similar to high elevation plots. Thus, the membership of plot x in the set of plots similar to high elevation plots, $\mu_C(x)$, is a weighted average of its similarity to high elevation plots, where the weights are the memberships of the other plots in the set of high elevation plots, $\mu_A(y)$. We used the Sørensen index, one recommended by Boyce and Ellison (2001), for S_{xy} in this study. The set of plots similar to low elevation plots (μ_D) is calculated similarly, with μ_B substituted for μ_A in equation (1). The set of plots similar to high-elevation plots while not similar to low elevation plots, or the apparent elevation (μ_E), is the anticommutative difference (Roberts, 1986) of μ_C and μ_D and is computed as

$$\mu_E(x) = \{(1 + [1 - \mu_D(x)]^2 - [1 - \mu_C(x)]^2)\}/2. \quad (2)$$

Equation (2) is related to the formula derived by Beals (1960) for calculating distances in polar ordinations, to which FSO is related, and is more fully described in Roberts (1987). The values of μ_E , or the apparent elevations, are then usually normalized to cover the full range from 0 to 1. Plots with a species composition typical of higher elevations will have higher apparent elevations than plots at the same

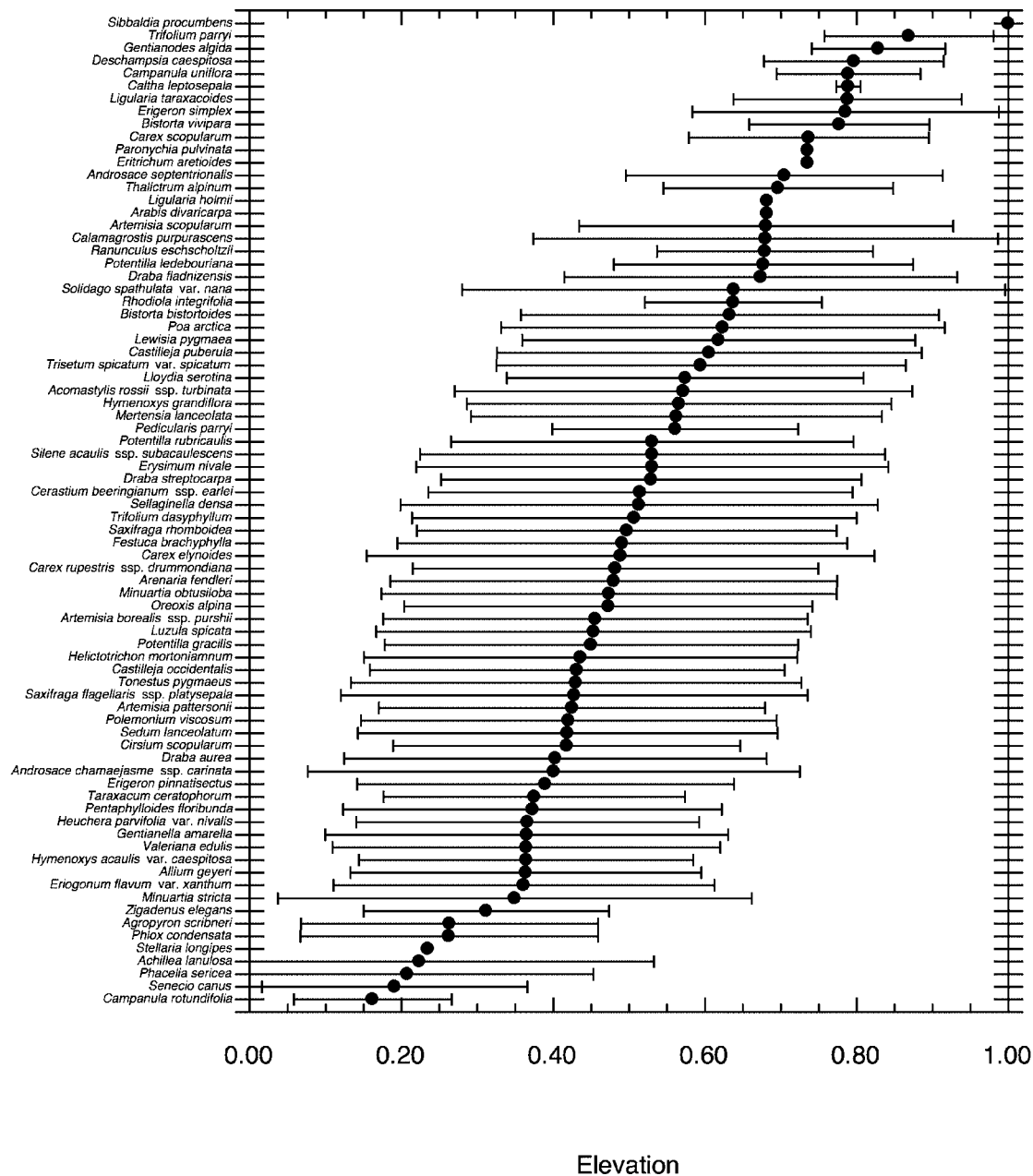


FIGURE 1. Mean fuzzy elevation (± 1 standard deviation) of each species. A fuzzy elevation of 1 = 3697 m, and a fuzzy elevation of 0 = 3561 m.

actual elevation with a species composition more typical of lower elevations. These apparent elevations can then be plotted against actual elevations to determine how much of the variation in species composition is explained by elevation (e.g., Boyce, 1998). Other anticommutative differences, using factors other than elevation, can be computed. In this study, sets of “apparent” factors, including elevation, were generated, by computing anticommutative differences, as described above. This differs from the original technique as developed by Roberts (1986) but appears to work better (see Discussion). The significance of each factor was assessed by calculating the rank correlation between the factor and its anticommutative difference, which was not affected by nonlinearities in the relationship. The critical *P*-value was adjusted using the Dunn-Sidak method (Day and Quinn, 1989) for the total number of factors examined. The apparent factors were also plotted against each other to see if the corresponding factors were correlated and thus described an underlying factor not measured in this study.

The kind of ordination described to this point operates in sample (site or plot) space and is sometimes called Q-mode ordination (Legendre and Legendre, 1998). Ordination can also be performed in species space (R-mode ordination), where, for example, S_{xy} is the similarity between species *x* and *y*, $\mu_A(y)$ is the membership of species *y* in the set of high elevation species, and $\mu_C(x)$ is the membership of species *x* in the set of species similar to high elevation species. A biplot can then be created with both site and species actual and apparent elevations and is presented in this study.

Results

The distributions of each species by elevation are shown in Figure 1. The beta diversity across this gradient was approximately 4.5 SD units (Gauch, 1982) or approximately 0.75 R units (Minchin, 1987), and so the step-across algorithms in FSO recommended for gradients with large beta diversities were not employed (Boyce and Ellison,

TABLE 1

Percent frequencies (presence) of each species. Nomenclature follows Weber (1976).

Species	Frequency (%)
<i>Achillea lanulosa</i>	12.7
<i>Acomastylis rossii</i> ssp. <i>turbinata</i>	66.7
<i>Agropyron scribneri</i>	31.7
<i>Allium geyeri</i>	28.6
<i>Androsace chamaejasme</i> ssp. <i>carinata</i>	33.3
<i>Androsace septentrionalis</i>	7.9
<i>Arabis divaricarpa</i>	1.6
<i>Arenaria fendleri</i>	65.1
<i>Artemisia borealis</i> ssp. <i>purshii</i>	76.2
<i>Artemisia pattersonii</i>	54.0
<i>Artemisia scopularum</i>	44.4
<i>Bistorta bistortoides</i>	60.3
<i>Bistorta vivipara</i>	15.9
<i>Calamagrostis purpurascens</i>	6.3
<i>Caltha leptosepala</i>	4.8
<i>Campanula rotundifolia</i>	7.9
<i>Campanula uniflora</i>	7.9
<i>Carex elynoides</i>	66.7
<i>Carex rupestris</i> ssp. <i>drummondiana</i>	39.7
<i>Carex scopularum</i>	12.7
<i>Castilleja occidentalis</i>	42.9
<i>Castilleja puberula</i>	3.2
<i>Cerastium beeringianum</i> ssp. <i>earlei</i>	23.8
<i>Cirsium scopularum</i>	36.5
<i>Deschampsia caespitosa</i>	22.2
<i>Draba aurea</i>	15.9
<i>Draba fladnizensis</i>	6.3
<i>Draba streptocarpa</i>	39.7
<i>Erigeron pinnatisectus</i>	25.4
<i>Erigeron simplex</i>	4.8
<i>Eriogonum flavum</i> var. <i>xanthum</i>	34.9
<i>Eritrichum aretioides</i>	1.6
<i>Erysimum nivale</i>	19.0
<i>Festuca brachyphylla</i> ssp. <i>coloradensis</i>	66.7
<i>Gentianella amarella</i>	6.3
<i>Gentianodes algida</i>	6.3
<i>Helictotrichon mortoniannum</i>	47.6
<i>Heuchera parvifolia</i> var. <i>nivalis</i>	23.8
<i>Hymenoxys acaulis</i> var. <i>caespitosa</i>	33.3
<i>Hymenoxys grandiflora</i>	17.5
<i>Lewisia pygmaea</i>	17.5
<i>Ligularia holmii</i>	1.6
<i>Ligularia taraxacoides</i>	3.2
<i>Lloydia serotina</i>	17.5
<i>Luzula spicata</i>	77.8
<i>Mertensia lanceolata</i>	50.8
<i>Minuartia obtusiloba</i>	77.8
<i>Minuartia stricta</i>	4.8
<i>Oreoxis alpina</i>	52.4
<i>Paronychia pulvinata</i>	1.6
<i>Pedicularis parryi</i>	4.8
<i>Pentaphylloides floribunda</i>	27.0
<i>Phacelia sericea</i>	9.5
<i>Phlox condensata</i>	6.3
<i>Poa arctica</i>	31.7
<i>Polemonium viscosum</i>	42.9
<i>Potentilla gracilis</i> ^a	77.8
<i>Potentilla ledebouriana</i>	3.2
<i>Potentilla rubraulis</i> ^b	47.6
<i>Ranunculus eschscholtzii</i>	4.8
<i>Rhodiola integrifolia</i>	7.9
<i>Saxifraga flagellaris</i> ssp. <i>platysepala</i>	31.7
<i>Saxifraga rhomboidea</i>	30.2
<i>Sedum lanceolatum</i>	68.3

TABLE 1

(Cont.)

Species	Frequency (%)
<i>Selaginella densa</i>	31.7
<i>Senecio canus</i>	20.6
<i>Sibbaldia procumbens</i>	1.6
<i>Silene acaulis</i> ssp. <i>subcaulescens</i>	34.9
<i>Solidago spathulata</i> var. <i>nana</i>	6.3
<i>Stellaria longipes</i>	1.6
<i>Taraxacum ceratophorum</i>	3.2
<i>Thalictrum alpinum</i>	20.6
<i>Tonestus pygmaeus</i>	4.8
<i>Trifolium dasyphyllum</i>	79.4
<i>Trifolium parryi</i>	12.7
<i>Trisetum spicatum</i>	33.3
<i>Valeriana edulis</i>	20.6
<i>Zigadenus elegans</i>	9.5

^a May also include individuals of *P. gracilis* × *hippiana*.

^b May also include individuals of *P. ovina*.

2001). Species frequencies are shown in Table 1. The most common species (present at $\geq 50\%$ of sites) were *Trifolium dasyphyllum*, *Luzula spicata*, *Minuartia obtusiloba*, *Potentilla gracilis*, *Artemisia borealis* ssp. *purshii*, *Sedum lanceolatum*, *Carex elynoides*, *Festuca brachyphylla* ssp. *coloradensis*, *Acomastylis rossii* ssp. *turbinata*, *Arenaria fendleri*, *Bistorta bistortoides*, *Oreoxis alpina*, and *Mertensia lanceolata*. The number of species per plot by elevation is shown in Figure 2. Species number dropped with increasing elevation, but the decrease was most marked above a fuzzy elevation of 0.75 (~3660 m).

Means and standard deviations of environmental factors are shown in Table 2. Several environmental factors were correlated with each other (Table 3). Soil carbon and nitrogen increased, and slope decreased, with elevation. Snow depth (SN) also increased with elevation. Aspect value (AV) was correlated with the C:N ratio, soil pH and the heat load index (HL), such that at cool northeasterly aspects, C:N increased and both pH and HL decreased. Soil texture (silt + clay fraction, or SICL) was not directly correlated with either elevation or aspect value, although it was correlated with some factors that were correlated with elevation, namely C, N, and pH. Thus, the factors

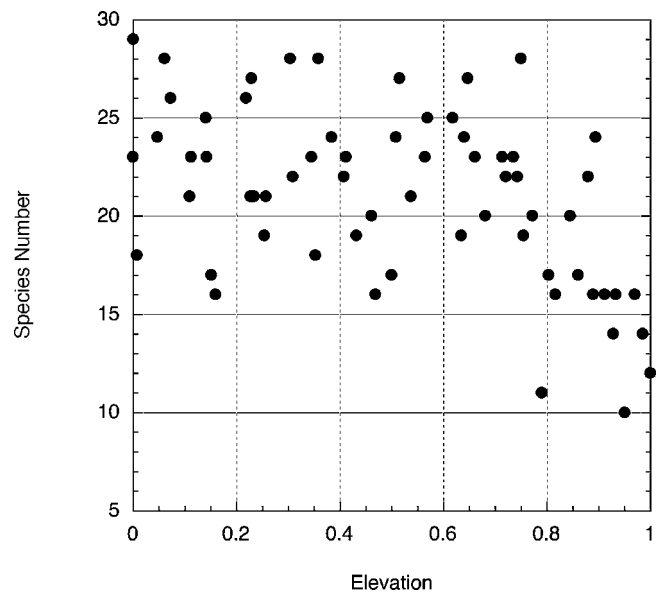


FIGURE 2. Number of species/plot vs. elevation. The relationship is significantly significant (Spearman $r = -0.48$, $P = 0.0002$).

TABLE 2

Means and standard deviations of environmental factors by exposure.

Factor	Both (N = 63)		East (N = 30)		West (N = 33)	
	Mean	SD	Mean	SD	Mean	SD
Elevation (m)	3630.8	41.2	3627.7	40.7	3633.7	42.1
Aspect (°)	359.5	55.8*	51.3	24.3*	306.6	34.9*
Slope (°)	14.8	5.1	14.8	4.0	14.7	6.0
Silt + Clay (%)	25.4	17.1	20.4	8.4	30.0	21.5
pH	5.3	0.4	5.1	0.4	5.6	0.3
C (%)	5.9	4.5	5.0	2.7	6.8	5.5
N (%)	0.44	0.33	0.34	0.18	0.54	0.40
Heat load (unitless)	0.87	0.08	0.80	0.05	0.93	0.05
Snow depth (cm)	28.2	32.4	26.5	36.8	29.7	28.3

* Angular deviation (Zar, 1984).

uncorrelated with each other that we used in the FSO were elevation, aspect value, and soil texture. We chose aspect value instead of heat load index because AV was better correlated with the C:N ratio and pH. We also included snow depth, although it was well correlated with elevation, because of its importance in other alpine sites in Colorado.

Actual elevation was well correlated with apparent elevation (Fig. 3A; Spearman $r = 0.73$, $P < 0.0001$). Aspect and apparent aspect were also well correlated (Fig. 3B; Spearman $r = 0.69$, $P < 0.0001$). However, soil texture was not correlated with apparent soil texture (Fig. 3C; Spearman $r = 0.15$, $P = 0.24$). In contrast, snow depth and apparent snow depth were well correlated (Fig. 3D; Spearman $r = 0.61$, $P < 0.0001$). The P -values of elevation, aspect, and snow depth were less than the Dunn-Sidak adjusted critical P -value of 0.013, so they were considered to be statistically significant relationships. The correlations of apparent gradients with each other were also examined. Apparent elevation, apparent soil texture, and apparent snow depth were highly correlated with each other (Fig. 4A–B), but apparent aspect value was not correlated with any of these factors (Fig. 4C).

Important environmental factors have not been evaluated with FSO in this way before. Therefore, as a check, we performed Bray-Curtis ordination on the data set. We used the variance-regression method of choosing end points, as recommended by Beals (1984). Elevation was most strongly correlated with the first axis but was also significantly correlated with the second and third axes (Table 4). Snow depth was strongly correlated with the second axis. The third axis was most strongly correlated with aspect value, followed by elevation and soil texture. However, neither elevation nor soil texture was considered statistically significant, as the Dunn-Sidak adjusted critical P -value of 0.013 was used. Polar ordination thus confirmed the importance of elevation, snow depth and aspect value.

We also performed R-mode (species space; Gauch, 1982) FSO, using the mean fuzzy elevations in Figure 1 to calculate species apparent elevation. Most of the species, especially the most abundant ones, fall along a fairly tight axis (Fig. 5). Apparent species elevation and actual mean elevation were well correlated (Spearman $r = 0.85$; $P < 0.0001$).

Discussion

Many of the correlations among factors were expected. Greater snow depth would be expected to increase soil moisture and decrease soil temperature, thus increasing both carbon and nitrogen. At northeasterly aspects, the C:N ratio increased, whereas both soil pH and the heat load index decreased. These aspects will, of course, receive less solar radiation and tend to be cooler and moister. These conditions are often associated with larger C:N ratios and more acidic soil pHs. Fine-textured soils retain moisture longer and thus are also often

TABLE 3

Correlations among environmental factors. Values listed are rank correlations (Spearman r). Values of r that are statistically significant at $P \leq 0.05$ are in bold. ELEV = fuzzy elevation, SL = slope, AV = aspect value = $(\cos(\text{aspect} - 45^\circ) + 1)/2$, SICL = silt + clay soil fraction, C = % soil carbon, N = % soil nitrogen, CN = soil C:N ratio, PH = soil pH, HL = heat load, SN = estimated snow depth.

	ELEV	SL	AV	SICL	C	N	CN	PH	HL	SN
ELEV	—	-0.44	-0.02	-0.03	0.51	0.49	0.11	-0.01	0.18	0.47
SL	-0.44	—	-0.15	0.01	-0.31	-0.29	-0.05	0.09	-0.35	-0.10
AV	-0.02	-0.15	—	-0.09	0.16	-0.03	0.64	-0.54	0.81	0.12
SICL	-0.04	0.01	-0.09	—	0.42	0.50	-0.24	0.25	0.10	0.21
C	0.51	-0.31	0.16	0.42	—	0.96	0.30	0.04	-0.08	0.36
N	0.49	-0.29	-0.03	0.50	0.96	—	0.05	0.13	0.09	0.38
CN	0.11	-0.05	0.64	-0.24	0.30	0.05	—	-0.38	-0.60	0.11
PH	-0.01	0.09	-0.54	0.25	0.04	0.13	-0.38	—	0.48	0.13
HL	0.18	-0.35	0.81	0.10	-0.08	0.09	-0.60	0.48	—	0.43
SN	0.47	-0.10	0.12	0.21	0.36	0.38	0.11	0.13	0.43	—

associated with higher soil organic matter (and thus more C and N) and higher soil pH. Some factors, such as slope, could not be examined as a separate factor, due to its strong negative correlation with elevation. This correlation was due to the shape of the saddle, with gentle slopes at the top and steeper ones below.

The strong correlations between elevation and other factors were unexpected. Temperature does decrease with elevation, so cooler temperatures at high elevations could inhibit decomposition and so increase soil carbon and nitrogen. Over an elevational gradient of ~140 m, however, the small declines in temperature should be outweighed by other factors. Even over larger gradients, elevation by itself is often not important in explaining alpine community distribution in Colorado (e.g., Komárková and Webber, 1978; Komárková, 1980; Isard, 1986) and elsewhere (e.g., Körner, 1999). Why then is elevation such an important determinant of plant community composition at Goliath Peak?

Elevation is positively correlated with snow depth (Fig. 6, Table 1), and snow depth is an important determinant of community type at Niwot Ridge (Walker et al., 1993). However, our study includes only a small subset of the total number of plant communities found at Niwot Ridge. Most of our sites appear to fall into the fellfield or *Carex elynoides*-dominated dry sedge meadow types (Komárková and Webber, 1978; May and Webber, 1982), which are the driest (Isard, 1986). Both of these community types have snow depth less than 50 cm (Walker et al., 1993). There were also a few moist and wet meadows (*sensu* May and Webber, 1982) at high elevations and gentle slopes, near the top of the saddle. Thus, by focusing on only a few community types, we removed much of the mesotopographic variation that is so important in alpine plant community determination (Körner, 1999). Elevation appears to be important mainly through its effect on increasing moisture. Additional support is given by the strong correlations among apparent elevation, apparent snow depth and apparent soil texture. Plots with high apparent elevation are similar in composition to high elevation plots, while not similar to plots at low elevations. We would expect these plots to be reflecting cooler or moisture conditions, or both. In a like manner, plots with apparent fine soil texture are similar to those with fine soil textures while not similar to those with coarse soil textures, and plots with high apparent snow depth are similar to those with high snow depth while not similar to those with low snow depth. Snow depth could have effects on both water availability and soil temperature; however, snow depths are relatively low at most of our sites, so snow depth should have an effect mainly on water availability. Since soil texture could only have a direct effect on water availability, not on temperature, and apparent soil

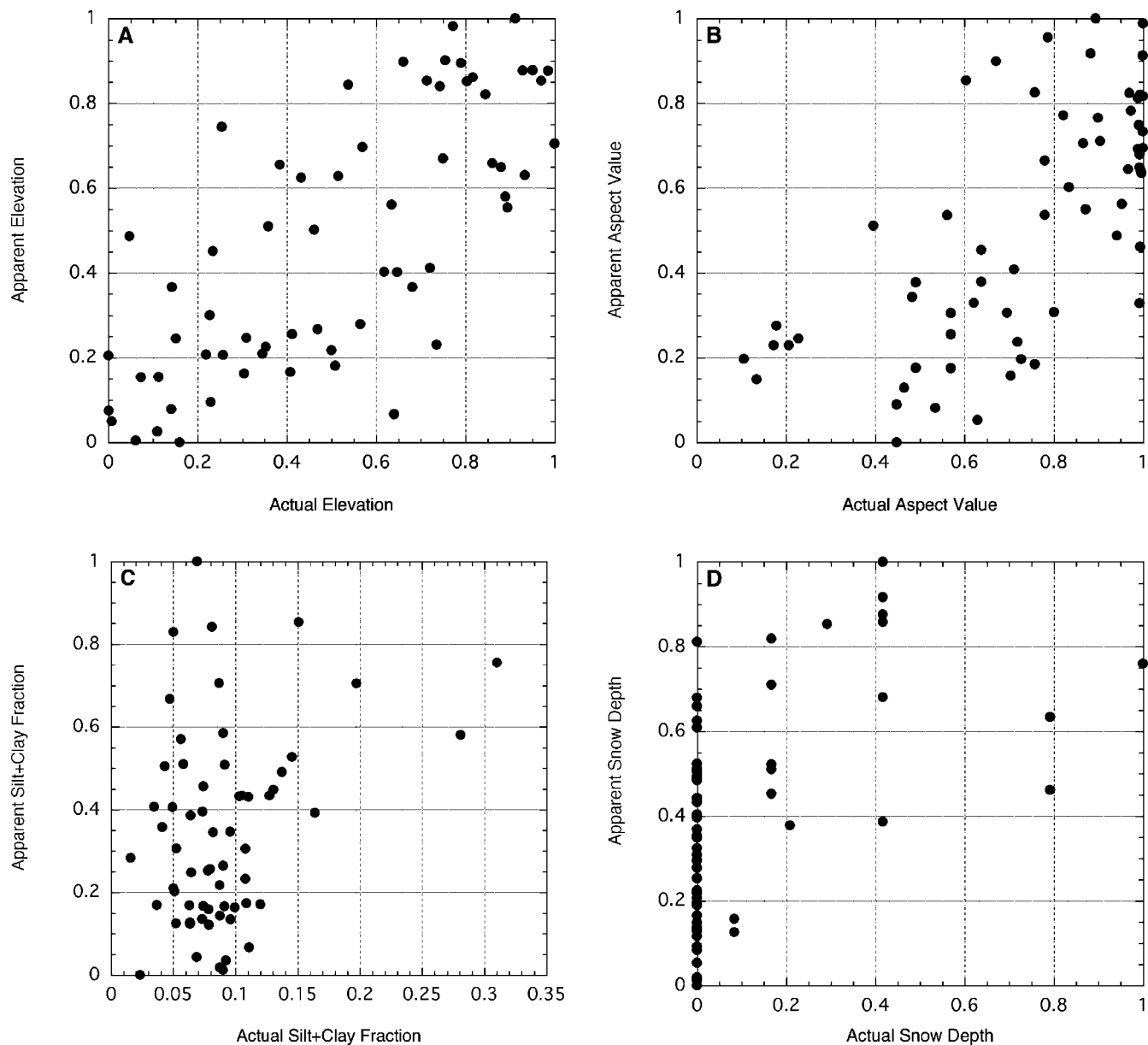


FIGURE 3. (A) Apparent elevation vs. actual elevation. Spearman $r=0.73$, $P < 0.0001$. (B) Apparent aspect value vs. actual elevation. Spearman $r=0.69$, $P < 0.0001$. (C) Apparent soil texture vs. actual soil texture. Spearman $r=0.15$, $P=0.24$. D: Apparent snow depth vs. actual snow depth. Spearman $r=0.61$, $P < 0.0001$.

texture is so strongly correlated with apparent elevation and apparent snow depth, plots with high apparent elevation and snow depth must be mainly moister, rather than cooler. Note that actual soil texture is not correlated with either elevation or snow depth (Table 3), so actual elevations, snow depths, and soil textures appear to be rough indicators of an underlying moisture gradient. Elevation and snow depth appear to be better predictors, since they are correlated with their apparent fuzzy sets, whereas soil texture is not correlated with apparent soil texture.

Aspect value may also have an effect on water availability—southwest slopes would be expected to be drier than northeast ones—but its effect appears to be primarily on temperature. Aspect value is not correlated with elevation, snow depth or soil texture, and apparent aspect value is not correlated with the corresponding apparent fuzzy sets. Thus, aspect value appears to reflect an underlying factor not shown by these factors, i.e., temperature. This is supported by the strong correlation between aspect value and heat load (Table 3).

Overall, our findings support earlier work in Colorado showing that snow cover and soil moisture are important factors determining

alpine plant distribution (Komárková and Webber, 1978; May and Webber, 1982; Isard, 1986; Walker et al., 1993). Additionally, our results show that these factors are also important within particular vegetation units. In order to test whether our findings were influenced by the moist and wet meadows found at the higher elevations, we carried out an ordination that included only the 45 sites with estimated snow depth between 0 and 25 cm. The relationships that we found between actual and apparent factors for this subset of data were similar to those found for the entire set of 63 sites (actual vs. apparent elevation—Spearman $r=0.59$, $P < 0.0001$; actual vs. apparent aspect value—Spearman $r=0.75$, $P < 0.0001$; actual vs. apparent soil texture—Spearman $r=0.09$, $P=0.56$). This indicates that species turnover within the fellfield and dry meadow types is driven by moisture gradients. Our findings also show that temperature, as reflected by aspect, has an effect within these vegetation units.

As was found by Hartman and Mitchell (1979), *Kobresia myosuroides* was not present on Goliath Peak. It appears to have been replaced here by the very similar *Carex elynoides*. *Kobresia*

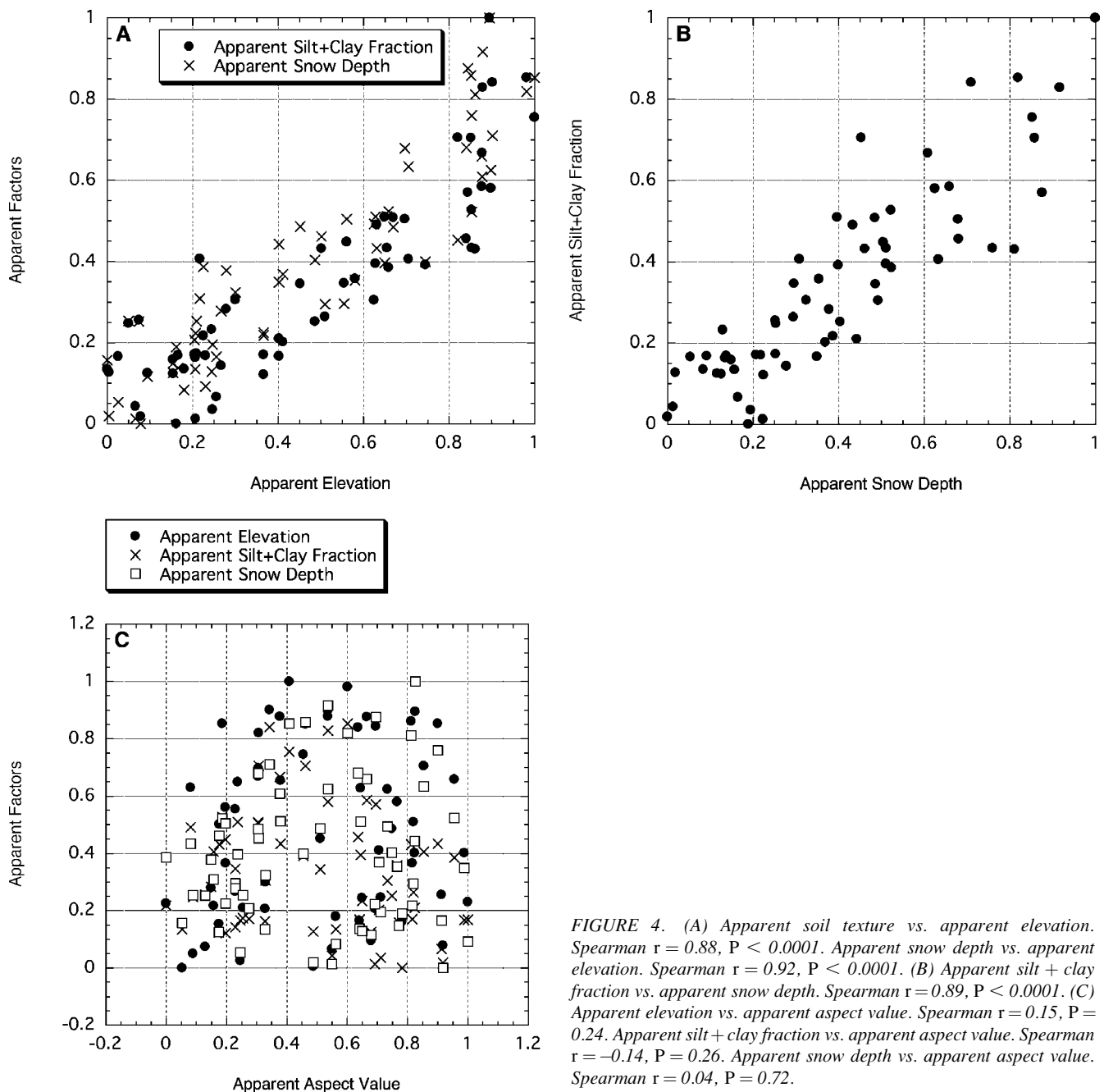


FIGURE 4. (A) Apparent soil texture vs. apparent elevation. Spearman $r = 0.88$, $P < 0.0001$. Apparent snow depth vs. apparent elevation. Spearman $r = 0.92$, $P < 0.0001$. (B) Apparent silt + clay fraction vs. apparent snow depth. Spearman $r = 0.89$, $P < 0.0001$. (C) Apparent elevation vs. apparent aspect value. Spearman $r = 0.15$, $P = 0.24$. Apparent silt + clay fraction vs. apparent aspect value. Spearman $r = -0.14$, $P = 0.26$. Apparent snow depth vs. apparent aspect value. Spearman $r = 0.04$, $P = 0.72$.

myosuroides is most dominant when snow depth falls in the 26 to 50 cm range (Walker et al., 1993). Few of the sites in our study have that snow depth, however (Fig. 7), which explain in part why *K. myosuroides* was not found in this study. *C. elynoides*-dominated dry meadows in the Indian Peaks are somewhat more xeric than *K. myosuroides*-dominated dry meadows (Komárková and Webber, 1978; Komárková, 1979; Walker et al., 2001). While we cannot determine community type directly from the data of our study, *C. elynoides* is found predominantly in areas with snow depths of 0 to 25 cm (Fig. 7).

Our east exposure roughly overlaps Hartman and Mitchell's Area #3, and many of the species noted by them were present in our study. However, they did note the presence of *Heterotheca villosa* (= *Chrysopsis villosa*) as a common species. We did not find this species; indeed, according to Weber and Wittmann (1996), this species would not be expected in the alpine at Goliath Peak, as it is generally found in foothill communities. One common species that we observed which was not mentioned by Hartman and Mitchell, however, was

Hymenoxys grandiflora. As both species have yellow flowers and are members of the same family, we think it likely that *H. grandiflora* was misidentified as *H. villosa* in the earlier study.

One disadvantage of using presence/absence data is that changes in total cover of plant species cannot be assessed. However, there are some advantages, as well. Since every species counts the same, the presence of rare species is effectively magnified. Turnover of these species is often more sensitive to environmental gradients, and ordination techniques may be more powerful in this case. Beals (1984) noted that presence/absence data sometimes performs better than abundance data.

Roberts (1986) originally proposed that FSO could be employed as combination of direct and indirect gradient analyses, in what was referred to as a heuristic approach. For example, after generating an apparent elevation set ($\mu_E(x)$), another set, $\mu_F(x)$, would be generated by taking the anticommutative difference of μ_E and μ_A (actual elevation), such that $\mu_F = \{(1 + [1 - \mu_A(x)]^2 - [1 - \mu_E(x)]^2)/2\}$. This set can be considered to be the "residuals" of a linear regression between

TABLE 4

Correlations among Bray-Curtis ordination axes and environmental factors. The Dunn-Sidak critical P-value is 0.013. Factors with P-values less than the critical value are shown in bold.

Axis	Factor	Spearman r	P
1	Elevation	0.73	<0.0001
	Aspect value	-0.09	0.48
	Soil texture	0.17	0.19
	Snow depth	0.63	<0.0001
2	Elevation	0.54	<0.0001
	Aspect value	0.17	0.19
	Soil texture	0.08	0.51
	Snow depth	0.41	0.0013
3	Elevation	-0.28	0.026
	Aspect value	0.35	0.006
	Soil texture	-0.29	0.025
	Snow depth	0.22	0.078

the apparent elevation μ_E and the actual elevation μ_A . In fact, there is a high degree of correlation between μ_F and $(\mu_A - \mu_E)$ in our data (Spearman $r = 0.93$; $P < 0.0001$). Roberts then proposed that this fuzzy set could be correlated against other environmental factors, and additional anticommutative differences could be taken for further testing against other gradients. In our data set, therefore, μ_F could be correlated against aspect value and soil texture. However, we did not find this to work well. The correlation of μ_F with aspect value was not significant (Spearman $r = 0.02$; $P = 0.86$). Using this approach, we would have overlooked the effect of aspect. When apparent aspect value was compared to actual aspect value, as presented in this study, the correlation was significant. Bray-Curtis ordination also found aspect value to be correlated with one of its axes (Table 4). Roberts' approach may not have worked for the following reason. Work with simulated data sets (Boyce and Weisenburger, unpublished data) has suggested that significant distortion occurs to "off-axis" points when an apparent fuzzy set is regressed against the actual gradient from

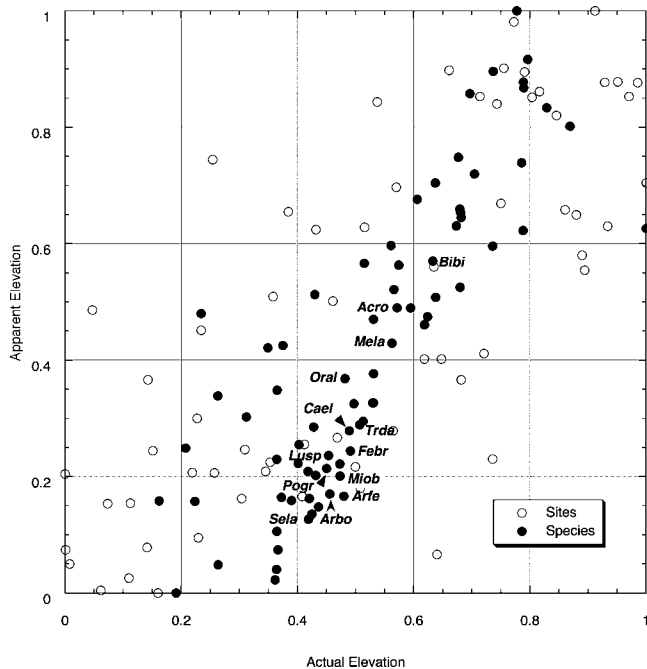


FIGURE 5. Species and site biplot of apparent vs. actual elevations. The most common species are denoted by a four-letter code that takes the first two letters from the generic and specific epithets in Table 1.

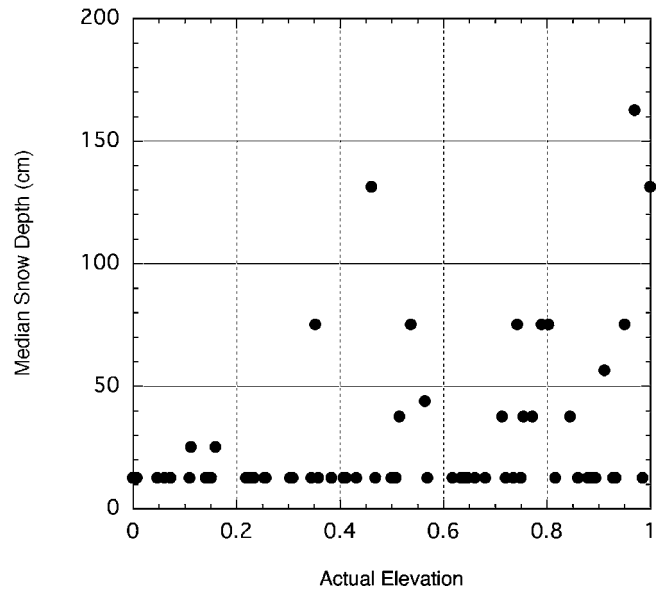


FIGURE 6. Median snow depth vs. elevation. Spearman $r = 0.47$, $P = 0.0002$.

which it was generated. Thus, while the assessment of the relationship is good (Boyce and Ellison, 2001), the precise position of off-axis points is a combination of variation due to other gradients and to distortion introduced by the ordination (as well as random error). Thus, we recommend that factors that are hypothesized to have an effect on community composition be ordinated one at a time, rather than in the successive manner proposed by Roberts (1986).

Our results confirm the findings of Boyce and Ellison (2001) that the Sørensen similarity index is an excellent index for FSO. Beals (1984) also recommended it for Bray-Curtis ordination. Boyce and Ellison (2001) also recommended the Baroni-Urbani & Buser index. In this study, however, we discovered that it is much more sensitive to species number than the Sørensen index (data not shown). This was not detected by Boyce and Ellison, as species number was not varied in their simulations. This property of the Baroni-Urbani & Buser index

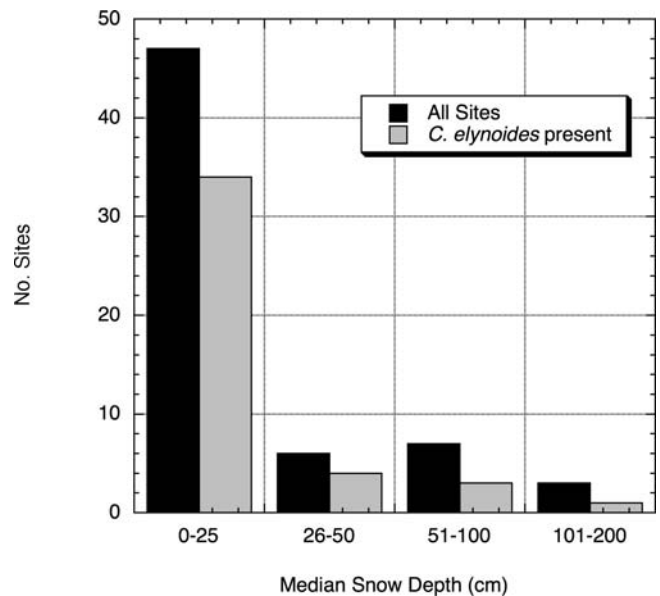


FIGURE 7. Distribution of sites across estimated snow depth classes. Both total number of sites and sites with *Carex elynoides* present are shown.

could be useful in the right circumstances, although we found that it led to outliers in the current study.

In conclusion, we found that water availability (as indicated by elevation, snow depth and (much less strongly) soil texture), and temperature (as indicated by aspect) were strongly associated with changes in plant community composition at Goliath Peak. Since many factors are correlated with both elevation (C, N, slope) and aspect (C:N, pH, HL), we cannot assign the cause of species turnover to these two factors, but we can state that changes in them are associated with species changes. We also showed that the Sørensen index was a very robust one to use with presence/absence data in FSO. We also showed that factors in FSO should be examined one at a time, rather than in the successive manner proposed by Roberts (1986), as the results are more congruent with polar ordination, the indirect gradient counterpart of FSO.

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