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High-elevation rock outcrop vegetation of the Southern Appalachian Mountains

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Abstract. Species composition patterns and vegetation-environment relationships were quantified for high-elevation rock outcrops of the Southern Appalachian Mountains, an infrequent and insular habitat in a forested landscape. Outcrops occur over a wide geographic range encompassing extensive variation in both geology and climate. Geographic-scale factors interact with site-scale factors to produce variation in vegetation among outcrops. Similarly, site-scale factors interact with micro-scale factors to produce variation in vegetation within outcrops. To provide a quantitatively-based classification of outcrop vegetation we used a TWINSPAN analysis of 154 100-m^2 plots. We recognized nine communities that primarily correspond to different combinations of elevation, bedrock type, geography, and moisture. Within outcrops of a single bedrock type, vegetation composition of 100-m^2 plots was consistently correlated with elevation and solar radiation, but relationships to soil nutrients varied with bedrock type. Both site-scale (100 m^2) factors (e.g. elevation, slope, aspect, and bedrock type) and plot-scale (1-m^2) microsite factors (e.g. soil depth, vegetation height, soil nutrients) were strongly correlated with species composition at the 1-m^2 level. Environment can be used to predict composition more effectively for 100-m^2 plots on a single bedrock type than either across bedrock types or at a 1-m^2 scale. Composition-environment relationships resemble those described for outcrop systems from other regions with pronounced topographic relief more than they do those described for the nearby but flatter and lower-elevation outcrops of the Southeastern Piedmont. There is strong spatial autocorrelation in this community, perhaps owing to dispersal limitation. Consequently, a comprehensive conservation strategy must include reservation of both a range of geologic types and a range of geographic locations.

Keywords: Correspondence Analysis; Disjunct distribution; Endemic species; Insular habitat; Partial ordination.

Nomenclature: Kartesz 1994, except for the recognition of *Houstonia longifolia* var. *glabra* Terrell.

Introduction

Rock outcrop vegetation in predominantly forested landscapes is generally insular and of infrequent occurrence. As a consequence, outcrop communities are of interest both because they harbor rare species and community types, and because they serve as a model system for study of patterns and processes in insular communities. The species composition of outcrop communities, like that of all vegetation, is influenced by multiple environmental factors that vary at differing spatial scales. Consequently, the influence of locally variable factors like aspect, slope, and elevation may be obscured by geographic-scale variation in geology and climate. Similarly, consistent relationships between small-scale compositional variation and microenvironment may be obscured by site-scale and geographic variation in environment. Consequently, attempts to generalize about vegetation-environment relations on outcrops require attention to sampling scale (see Larson et al. 1989). Inconsistencies among the patterns previously described for outcrop vegetation (e.g. the importance of soil depth vs. geology vs. topography) may result from inconsistencies in sampling scale (cf. 1-m^2 plots of Maycock & Fahselt 1992 vs. 25-m^2 plots of Burgman 1987 and 100-300-m^2 relevés of Makirinta 1985) and the range of environmental variation (particularly of bedrock types) examined (cf. Ashton & Webb 1977 and Maycock & Fahselt 1992 vs. Sharitz & McCormick 1973; Collins et al. 1989).

Within the Southern Appalachian landscape, high-elevation (> 1200 m a.s.l.) rock outcrops are uncommon, spatially isolated from each other, and possessed of one of the richest floras of rare species of any habitat in the region. These rare species, which include numerous endemics as well as disjuncts from far to the north, indicate that the outcrop vegetation may harbor remnants of a now largely vanished Pleistocene alpine flora (Ramseur 1960; White et al. 1984; Billings 1988). Their limited extent, limited economic importance, and frequent inaccessibility has resulted in these outcrops being little studied in contrast to other vegetation in the region.

This paper describes the vegetation of Southern Appalachian high-elevation outcrops and how composition varies with environment and geography. These relationships are examined at several spatial scales to

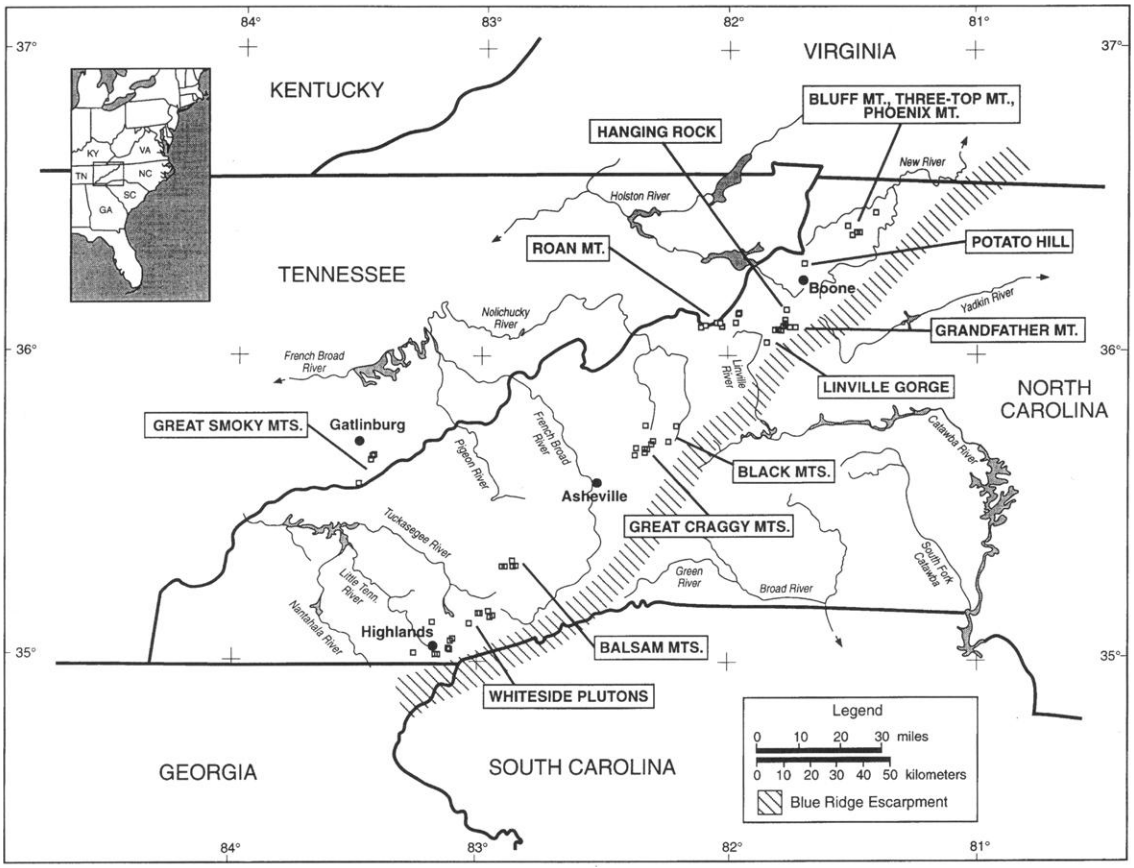

Fig. 1. Map of study area showing plot locations (small squares), major peaks and bedrock types.

address the following questions. (1) Do vegetation-environment relationships vary with scale of observation? (2) Do vegetation-environment relationships vary with the geographic extent of the area considered, and if so, what environmental factors are important when vegetation is studied over large areas? (3) To what extent are vegetation-environment correlations consistent across bedrock types and across the region? (4) To what extent are these observed correlations consistent with those observed in outcrop vegetation studied outside the region?

Study area

This study includes Southern Appalachian high-elevation outcrops > 100 m^2 in area and > 1200 m a.s.l. in the high peaks region of western North Carolina and eastern Tennessee, (between 35° and 37° N; Fig. 1). Sites > 1200 m are thought to have been near or above treeline during the last glacial maximum (Delcourt & Delcourt 1985, 1988). Except for Mt. Rogers peaks > 1200 m do not occur North of the Virginia-North Carolina state line. The absence of high peaks and associated Pleistocene alpine vegetation causes a natural biogeographic boundary.

The regional terrain consists of typically rounded, forested summits; more rarely peaks have a rugged relief with rock outcrops present (Fenneman 1938). High-elevation outcrops occur on rocks that range in composition from felsics like granite, gneiss and schist to mafics like gabbro and amphibolite, all largely of Precambrian origin (Table 1). Mafic rocks have higher iron and magnesium content and lower aluminum content than do felsic rocks, and generally weather to more fertile soils. Mafic rocks are most frequent in the northern part of the study area. Rock outcrop soils are generally lumped in the USDA classification as Entisols or Lithic Haplumbrepts (Brady 1984).

Few meteorological stations occur on the high peaks, but available data suggest that mean annual precipitation ranges from 1270 to 2000 mm (Shanks 1954; Ruffner 1985), generally increasing with elevation. Most precipitation comes from southwesterly winds, resulting in a southwest to northeast gradient of decreasing precipitation (Dickson 1959). Precipitation is season-

Table 1. Summary of bedrock types in the study area.

Bedrock type	Geographic area	No. plots
Mafic		
Amphibolite	Three Top Mt., Bluff Mt., Phoenix Mt., Potato Hill	28
Metagabbro	Roan Mt. Massif	13
Metabasalt	Hanging Rock	3
Intermediate		
Meta-arkose	Grandfather Mt., Linville Gorge (Hawksbill Mt.)	26
Felsic		
Quartzite	Linville Gorge (Table Rock)	1
Metagraywacke	Great Craggy Mts., Black Mts.	27
Muscovite-biotite gneiss	Balsam Mts.	9
Anakeesta sulfitic slate	Great Smoky Mts.	16
Sandstone and conglomerate	Great Smoky Mts.	1
Whiteside quartz-diorite	Vicinity of Highlands, North Carolina	30

ally bimodal with peaks in mid-summer and mid-winter, and a low in the autumn. Mean July temperatures are cool for the region (17 °C at 1618 m and 15 °C at 1991 m). Frosts occur from late September to mid May. On Grandfather Mountain, one of the region's most exposed peaks, mean wind speed ranges from 18.5 km/hr in the summer to 33 km/hr in December, with gusts to 270 km/hr recorded (data provided by Grandfather Mt, Inc.).

Although the highest peaks of the Southern Appalachians are now forested to their summits, it is likely that climatic treeline occurred near 1450 m during the full glacial (ca. 18 000 B.P.; Delcourt & Delcourt 1985, 1988). On exposed, windy peaks the treeline is usually lower so the 1200 m sampling cutoff roughly matches the lower distributional limit of the putative Pleistocene alpine relicts. As climates warmed, treeline and true alpine vegetation moved upward, but likely persisted in the region until ca. 12 500 B.P. (Delcourt & Delcourt 1985, 1988).

Despite the long absence of a climatic treeline, high-elevation outcrops support plant species with strong alpine and arctic affinities (Wiser 1994), such as *Geum radiatum*, *Juncus trifidus* and *Sibbaldiopsis tridentata*. Much of the rest of the outcrop flora is adapted to open, treeless habitats that have abundant sunlight (cf. Baskin & Baskin 1988; Wiser 1994). Vegetation surrounding high-elevation outcrops includes *Picea-Abies* forest and grassy balds at the highest elevations (> 1550 m), with northern hardwood forest (dominated by *Fagus grandifolia* and *Betula alleghaniensis*) or oak forest (*Quercus rubra* and *Q. prinus*) at the lower elevations (1200 - 1800 m). Heath-dominated shrublands occur as surrounding vegetation over a broad range of elevations.

Data collection

Study sites were located on 42 peaks in 11 localities (Fig. 1) selected to maximize the number of combinations of rock type, elevation, aspect, longitude, and latitude sampled. Potential sites were identified by visual reconnaissance, searches of published and unpublished literature, aereal photographs, topographic maps, and personal recommendations. Outcrops were required to have herbaceous plant species as a prominent component of the vegetation, > 5 % of the area as exposed bedrock, and > 75 % of the area with bedrock within 20 cm of the surface. Sites ranged from large, rocky ridges and cliff-faces with little forest in view and minimal shading, to protected sites at cliff bases or seepage slopes surrounded by forest and at least partially shaded. Grassy balds, severely trampled outcrops, and sites requiring technical climbing equipment were excluded from this study.

Plots of 10 m × 10 m (100-m^2) were sampled for comparisons between outcrops and between localities on a given outcrop, whereas 1 m × 1 m (1 m^2) subplots were sampled to examine microhabitats within outcrops. The larger plot was visually stratified into types according to vegetation height and dominant growth form (i.e. woody, graminoid, forb), and 1-2 1-m^2 subplots were randomly placed within each type. Two to seven 1-m^2 subplots were sampled within each 100-m^2 plot, depending on vegetation heterogeneity. At both plot and subplot levels, all vascular plant species were recorded and cover estimates made by SKW using the ten-class cover scale of Peet et al. (1990): 1 = < 0.1 %; 2 = 0.1 - 1 %; 3 = > 1 - 2 %; 4 = > 2 - 5%; 5 = > 5 - 10 %; 6 = > 10 - 25 %; 7 = > 25 - 50 %; 8 = > 50 - 75 %; 9 = > 75 - 95 %; 10 = > 95 - 100 %). This scale was designed to allow accurate estimation to within one class and to be interconvertible with other commonly used cover scales. A total of 154 100-m^2 plots and 596 1-m^2 subplots were sampled. Voucher specimens have been deposited at NCU. Plot data are available upon request.

Site parameters measured on 100-m^2 plots

Near the center of each 100-m^2 plot, latitude, longitude, elevation, slope and aspect were determined. Topographic position was recorded as an index from 1 to 10 with 1 being the outcrop base and 10 being the outcrop summit. Percent exposed bedrock was estimated visually. Outcrops were categorized by vertical relief (1 = < 5 m high; 2 = 5-16 m; 3 = 16-32 m; 4 = 32 - 64 m; 5 = > 64 m). A three-point rock surface fracturing index was defined ranging from nearly smooth outcrops with ledges and cracks < 0.3 m wide designated '1', to highly fractured and angular outcrops with ledges and cracks > 0.3 m wide designated '3'. Horizontal and vertical distance to the nearest landform or vegetation higher than the plot were estimated in four directions from the plot center (towards, opposite and perpendicular to the direction of maximum exposure). Surrounding vegetation was classified following Schafale & Weakley (1990) as *Picea-Abies* Forest, Northern Hardwoods Forest, Heath Bald, Grassy Bald, High-Elevation Red Oak Forest, Chestnut Oak Forest, or Pine-Oak Heath.

Samples of dominant rock types were collected on each plot, and identified by Charles Troop, Dept. of Geology, University of North Carolina at Chapel Hill. Plots were then classed as mafic, felsic, or intermediate (intermediate included felsic outcrops with frequent veins or small intrusions of mafic rock).

Outcrop area was classified from measurements on orthophoto quadrangle maps as: 1 = not visible; 2 = visible and < 0.25 ha; 3 = 0.25-1.0 ha; 4 = 1-9 ha; 5 = 9-25 ha, 6 = > 25 ha.

Site parameters measured on 1-m² subplots

Percent slope, topographic position index, distance and height to protecting landforms or vegetation, and maximum vegetation height were determined for each 1-m^2 subplot. Average soil depth was calculated based on 16 measurements taken on a grid within each subplot using a graduated steel pin. Percent sky obstructed by rock ledges or vegetation was measured using a spherical densiometer (Lemmon 1956). Percent cover of lichens, mosses, rock and bare soil were estimated visually. Potential water sources were recorded (perennial seepage, drip or runoff from above, direct precipitation).

In each subplot, soil samples were collected from the top 10 cm of soil below the litter layer. Soils were air-dried, sieved and analyzed for pH, percent organic matter and available potassium, calcium, magnesium, phosphorus, sulfate, sodium, copper, boron, iron, manganese, aluminum, and zinc (Mehlich 3 extractant, Mehlich 1984; Brookside Laboratory Association, Inc., New Knoxville, OH). Percent organic matter was determined by loss-on-ignition, and moisture holding capacity as water held in fully saturated soil as a percent of dry weight. Soil parameter values were averaged across component 1-m^2 subplots to provide a representative value for each 100-m^2 plot.

Data analysis

Calculated site parameters and indices

Principal Components Analysis (PCA) on plot longitude and latitude was used to determine relative position on the long (NE - SW) axis of the mountains, and relative position on the shorter (SE - NW) axis of the mountains.

Potential solar beam irradiation was calculated based on slope, aspect and latitude (Frank & Lee 1966). Aspect was transformed into a linear variable (Beers et al. 1966) where the optimal aspect for growth of a given species or vegetation type ($A_{\max}$) was assigned the maximum value of 2.00, and the opposite direction was assigned a value of 0.00. Aspects were calculated as

$$A' = \cos(A_{\max} - A) + 1, \qquad (1)$$

where A is the measured aspect in degrees and A' is the transformed aspect code. A procedure analogous to that of Dargie et al. (1987) was used to determine the optimal $A_{\max}$ (=10°) with subsequent increments 20, 5, and 1 tested to find the best fit to a Canonical Correspondence Analysis constrained to be the maximum fit to the transformed aspect (cf. Reed et al. 1993).

Two exposure indices were calculated for each plot and subplot. The first is a modification of that of Callaway et al. (1987):

$$\text{protection} = 0.25 \sum \left((ER - EP)/D \right) \qquad (2)$$

where ER = elevation of structures higher than the plot; EP = plot elevation; D = distance from plot to the higher structure, averaged over observations made at four 90° intervals with one being in the direction of the plot's maximum downward slope. If the plot was located on a rockface whose slope extended above the plot, that rockface was assumed to protect the plot on its surface from exposure in that direction.

Because exposure is not linearly related to the height and distance of protecting structures, we calculated a second index (P. Robinson, UNC Geography Dept., pers. comm.). Exposure in each of the four 90° intervals examined was defined as '1' (totally protected) when the height of neighboring landforms or vegetation was greater than 10 times the distance to the plot, as '5' (totally exposed) when their height was less than 0.1 times the distance to the plot, or '3' when they were intermediate in height relative to distance to the plot. Scores were averaged to produce a plot exposure index ranging from 1 (fully protected) to 5 (fully exposed).

To satisfy normality assumptions of some statistical analyses, water holding capacity, manganese, copper, zinc, organic matter, calcium, phosphorous, magnesium, sodium and sulfate were log-transformed, and iron and potassium were square-root transformed (100-m^2 plots). For 1-m^2 subplots the transformations were identical, except that iron was not transformed and boron was log-transformed.

To reduce collinearity and facilitate interpretation of

Table 2. Loadings of soil parameters on the first five axes of the varimax-rotated PCA. The highest loading for each soil parameter is in bold. Units for all variables are ppm except pH, organic matter (%), and water holding capacity (% dry weight). Cum var. = Cumulative % variance explained.

Axis Name	Cations	Soil Moisture	Iron Axis	pH Axis	Sulfate Axis
	100-m^2 plots, $N = 154$				
pH	0.15	– 0.27	0.13	**0.82**	– 0.13
Boron	0.39	0.05	**0.71**	0.20	0.03
Aluminum	– 0.32	– 0.02	0.06	**0.61**	0.50
Sqrt (iron)	– 0.29	0.04	**0.76**	– 0.03	– 0.08
Sqrt (potassium)	0.51	**0.62**	0.03	0.19	0.19
^{e}log (calcium)	**0.91**	0.08	– 0.05	– 0.13	– 0.04
^{e}log(copper)	0.11	– 0.22	**0.67**	0.04	0.14
^{e}log(magnesium)	**0.85**	0.09	0.03	0.18	– 0.21
^{e}log(manganese)	**0.72**	0.17	0.23	0.16	0.06
^{e}log(sodium)	– 0.00	0.42	– 0.02	**0.71**	– 0.17
^{e}log(organic matter)	0.21	**0.92**	0.01	– 0.12	– 0.07
^{e}log(phosphorus)	0.15	– 0.30	– 0.27	– 0.19	**0.72**
^{e}log(sulfate)	– 0.12	– 0.06	0.43	– 0.05	**0.78**
^{e}log(water hold.cap.)	0.05	**0.83**	– 0.07	0.09	– 0.20
^{e}log (zinc)	**0.81**	0.22	– 0.13	– 0.27	0.07
Cum. var.	28.8	44.6	58.7	68.5	76.6

1-m^2 plots, $N = 577$

Axis Name	Cations	Soil Moisture	Sulfate Axis	pH Axis	Iron Axis
pH	0.21	– 0.20	0.01	**0.86**	– 0.02
^{e}log (boron)	0.41	0.04	0.28	0.19	**0.68**
aluminum	– 0.46	0.03	**0.48**	0.46	– 0.06
iron	– 0.22	– 0.03	0.11	– 0.15	**0.85**
Sqrt (potassium)	0.46	**0.68**	0.21	0.08	0.07
^{e}log (calcium)	**0.92**	0.12	– 0.08	– 0.01	– 0.10
^{e}log (copper)	0.15	– 0.21	**0.54**	0.17	0.25
^{e}log (magnesium)	**0.86**	0.17	– 0.11	0.19	0.07
^{e}log (manganese)	**0.76**	0.17	0.10	0.20	0.06
^{e}log (sodium)	0.04	0.43	– 0.14	**0.62**	0.10
^{e}log (organic matter)	0.24	**0.90**	– 0.06	– 0.06	0.09
^{e}log (phosphorus)	0.14	– 0.12	**0.57**	– 0.31	– 0.53
^{e}log (sulfate)	– 0.20	0.04	**0.86**	– 0.16	0.15
^{e}log (water hold. cap.	0.03	**0.73**	– 0.06	0.06	– 0.07
^{e}log (zinc)	**0.80**	0.32	– 0.04	– 0.16	– 0.15
Cum. var.	0.30	0.43	0.55	0.66	0.74

soil differences, soil nutrient variation was reduced to five principal components. A VARIMAX rotation was employed to produce a more interpretable structure (Dunteman 1989). The first five PCA axes account for 76.6 % of the soil nutrient variation among 100-m^2 plots and 73.8 % of the variation in soil nutrients among 1-m^2 subplots (Table 2). Axis names derive from the soil parameter with the highest loadings on that axis.

Classification and ordination

To first examine compositional variation, TWINSPAN (Hill 1979, see review in Kent & Ballard 1988) was used to classify the outcrop vegetation data from the 100-m^2 plots into communities. The program was run using default options, except that pseudospecies cut levels (*sensu* Hill 1979) used were 5 % and 50 % cover. As TWINSPAN requires splits at each iteration and distance down the hierarchy is not related to group homogeneity, we chose final division levels to maximize interpretability of communities in terms of major environmental and geographic gradients. To assure the robustness of the resultant classification, we devised a second classification using Sørensen's similarity coefficient with the group average linkage cluster analysis algorithm. This produced nearly identical results to the TWINSPAN analysis. Constancy (i.e. percent of plots of a community with species present) and mean cover in plots of occurrence were calculated for both prevalent species (i.e. those *n* species with the highest constancy, where *n* equals the mean species richness for the community; see Curtis 1959), and regionally rare species. Homoteneity (*sensu* Peet 1981), an index of the relative uniformity of a community type, was calculated for each type as the sum of the constancy values of the prevalents divided by the sum of the constancy values of all the species (Curtis 1959; Peet 1981).

Vegetation-environment relationships were examined using Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), partial DCA and partial CCA. All runs of DCA used detrending by segments and non-linear rescaling as advocated by Knox (1989). Correlations between environmental variables and ordination axes were assessed using Pearson's correlation coefficient. CCA adds the constraint that ordination axes must be linear combinations of measured environmental variables (ter Braak 1987, 1988). DCA and CCA eigenvalues provide a measure of the amount of variation in the species data accounted for by each axis; the total inertia (eigenvalues summed across all axes) indicates the total variance in the species data accounted for by the ordination. With CCA, the sum of canonical eigenvalues indicates the amount of variation explained by the site parameters supplied (ter Braak 1988). Monte Carlo permutations were applied to CCA analyses to determine if the strength of species sorting along the environmental variables was greater than would be expected by chance (ter Braak 1988; Crowley 1992).

Interpretation of compositional variation among 1-m^2 subplots may be complicated by overall 100-m^2 plot differences. Ter Braak (1986) suggested using partial ordination, a technique allowing designated variables to be treated as covariables, to analyze nested data. Variation in the species by site matrix accounted for by covariables is subtracted from the data before extraction of ordination axes, thereby allowing examination of strictly small-scale variation. Partial DCA of the 1-m^2 data, with scores on DCA axes 1 - 4 for the 100-m^2 plot to which the 1-m^2 subplot belonged as covariables, allowed analysis of subplot-scale variation and its relationship to environmental variation measured at this scale.

An approach analogous to that of Borcard et al. (1992) was used to quantify species patterns that reflect differences among microhabitats from those reflecting site differences. Toward this end, four analyses were made of the 1-m^2 subplot data. First, two separate CCA analyses were conducted. CCA analysis 1 was constrained by DCA scores for the 100-m^2 plots, and thus represents the variation contained in the 100-m^2 plots where some is specific to the 100-m^2 scale and some is shared with the 1-m^2 scale owing to spatial autocorrelation. CCA analysis 2 was constrained by site parameters measured on 1-m^2 subplots, and thus represents the variation attributable to environmental data collected at the 1-m^2 scale, some of which is specific to the 1-m^2 scale and some of which is shared with the 100-m^2 scale owing to spatial autocorrelation. Next, two partial CCA ordinations were conducted. Analysis 3 used DCA scores for the 100-m^2 plots as covariables and constrained remaining variation by measured site parameters, with the result that this analysis is influenced only by information exclusively present at the 1-m^2 level. Analysis 4 used site parameters as covariables and constrained the CCA by 100-m^2 DCA scores, with the result that the analysis is influenced only by information exclusively present at the 100-m^2 level. The percent of the total variation of species data accounted for by each analysis is obtained by dividing the sum of the canonical eigenvalues by the total inertia and multiplying by 100. By adding this value for analyses 1 and 3 or for 2 and 4, the total amount of explained variation in the data is obtained. This can be partitioned as: (a) that accounted for by differences among 100-m^2 plots only [analysis 4], (b) that accounted for by site parameters measured on 1-m^2 subplots only [analysis 3] , (c) that shared by the two plot sizes [step 2 - step 3, or step 1 - step 4], and (d) unexplained variation and stochastic fluctuations [100 - total explained variation]. Although an analogous approach employing dummy variables to indicate plot membership to examine subplot differences would have been possible (Palmer 1990; Lavorel et al. 1991), the large number of plots analyzed here would have required unreasonable numbers of dummy variables.

'Stepwise' CCA selected from five to nine microenvironmental variables in the analyses partitioned by bedrock type and 19 microenvironmental variables for the complete data set. All the selected microenvironmental parameters were retained as the primary goal was to determine the maximum amount of variation they could explain (cf. Økland & Eilertsen 1994).

To determine if environmental gradients influencing vegetation were the same on different bedrock types and if patterns varied with geographic extent, the datasets were partitioned by bedrock type (see Peet 1981). Plots and subplots having seepage were deleted from this portion of the analysis as seepage influenced both soils and vegetation, but occurred inconsistently across bedrock types. At least 10 100-m^2 plots and 30 1-m^2 subplots remained in six of the bedrock types. These six included two mafic (amphibolite and metagabbro), one intermediate (meta-arkose) and three felsic types (metagraywacke, Anakeesta slate, Whiteside quartz-diorite).

CCA was also used to compare abilities of the two exposure indices to explain variation in compositional data (see Reed et al. 1993). Two analyses were conducted, each constrained by one exposure index. For both plot sizes, the second exposure index explained more of the variation in the species data, and consequently was used in all analyses.

DCA and CCA ordinations and Monte Carlo tests were performed using the computer package CANOCO (version 3.10, ter Braak 1990). Ordination biplots were produced using SYGRAPH (version 5.0, Wilkinson 1990). TWINSPAN and cluster analysis were performed using the computer package PC-RECCE (Hall 1992). Other statistical analyses were performed using SAS (version 6.04, Anon. 1987).

Results

294 vascular plant species were encountered in 154 100-m^2 plots. Species richness averaged 18 per 100-m^2 plot and 6 per 1-m^2 subplot.

Nine TWINSPAN communities were selected to characterize the high-elevation outcrop vegetation (Figs. 2 and 3, Table 3). Although the TWINSPAN divisions partly reflect geographic position, local site factors also strongly influence composition. Within each locality (Fig. 1), this resulted in delineation of 2 to 5 communities. Only one community is restricted to a single locality and no one community occurs on all.

The first TWINSPAN dichotomy differentiated vegetation types according to elevation (Figs. 2-4). Among higher elevation communities, further divisions correspond to additional partitioning by elevation, geography, geology and presence of abundant seepage (Fig. 2). Among lower elevation communities, further divisions distinguish communities that differ in geography or bedrock type. Highest species richness (37 - 43 species per 100-m^2 plot) occurred in communities on mafic bedrock at 1320 - 1360 m. The two communities with the lowest species richness occur at the highest elevations (Table 3).

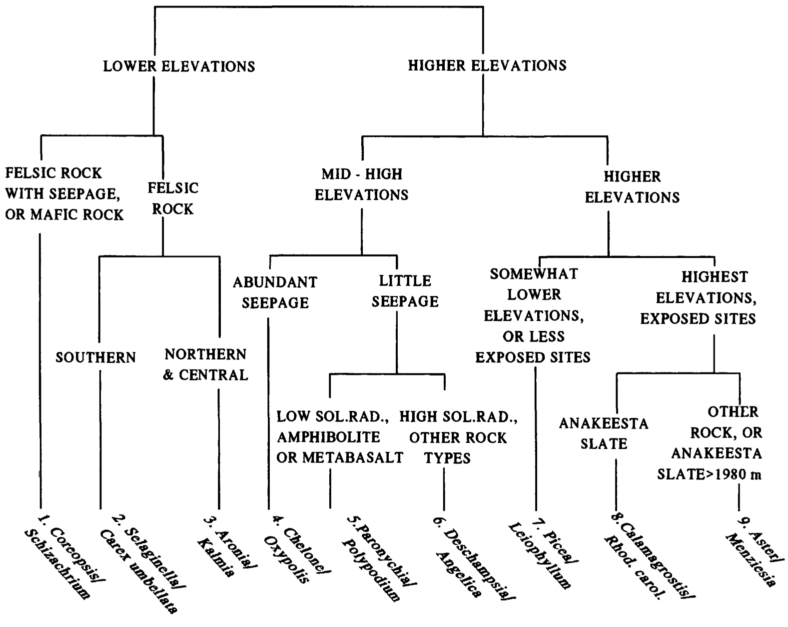

Fig. 2. Hierarchical relationships of TWINSPAN communities and associated environmental contrasts.

Community characterization

Community names employed below derive from two species that have constancy greater than 55 % which distinguish the community by either their presence or high constancy.

Carex misera, *Saxifraga michauxii* and *Vaccinium corymbosum* have high constancy and occur in all community types, which may be explained by their ability to readily invade disturbed outcrops. *Scirpus cespitosus*, *Sorbus americana*, *Rhododendron catawbiense*, *Polypodium appalachianum* and *Agrostis perennans* each occur in eight of the nine communities.

The *Coreopsis major-Schizachyrium scoparium* outcrop community occurs at low-to-mid elevations (1250-1700 m) on mafic rock, or felsic rock with perennial seepage. Soils have higher pH, magnesium and manganese than do those from other outcrop communities. *Saxifraga michauxii*, *Quercus rubra*, *Dichanthelium acuminatum*, *Kalmia latifolia*, *Danthonia spicata* and *Paronychia argycoma* have high constancy. When present on outcrops, *Allium cernuum*, and the regionally rare *Muhlenbergia glomerata* and *Heuchera longiflora*, occur only in this community (Table 3). Surrounding vegetation is predominantly deciduous forest with *Q. rubra*, *Acer rubrum* and *Tsuga caroliniana*. On steeper slopes and at slightly higher elevations on the same peaks, this community is replaced by the *Paronychia argycoma-Polypodium appalachianum* community (see below).

The *Selaginella tortipila-Carex umbellata* outcrop community usually occurs below 1600 m on felsic bedrock and is primarily confined to the southern part of the study area. It predominates on Whiteside quartz-diorite outcrops, locally referred to as 'granite domes'. These smooth, south-facing outcrops with shallow slopes ($\bar{x}$ = 26°) are typically dominated by *Selaginella tortipila* mats, comprising 20 to 100 % of the total cover. Soils tend to be lower in major cations and micronutrients than those of the other communities. Mid-summer drought stress is marked. *Krigia montana*, *Dichanthelium acuminatum*, and *Houstonia longifolia* var. *glabra* reach their highest constancy here. On the outcrops studied, the regionally rare *Juniperus communis* var. *depressa* occurs only in this community. Surrounding vegetation is predominantly deciduous forest with *Quercus rubra*, *Q. prinus*, *Q. alba*, *Pinus rigida*, *P. strobus* and *Acer rubrum* dominant, and an understory of ericaceous shrubs including *Rhododendron* spp., *Kalmia latifolia*, *Vaccinium* spp. This community occurs less commonly north of the Black Mts. (Fig. 5, below) owing to the scarcity of smooth, flat outcrops on relatively low-elevation ridgetops.

The *Aronia arbutifolia-Kalmia latifolia* outcrop community occurs on shallow slopes ($\bar{x}$ = 27°) over felsic bedrock at low-to-mid elevations (1200-1700 m). South of Asheville, this community is encountered under environmental conditions uncommon there – either at low elevations on north-facing slopes or at high elevations on south-facing slopes where *S. tortipila* is sparse or absent. *Amelanchier arborea*, *Scirpus cespitosus*, *Acer rubrum*, *Rhododendron catawbiense*, *Leiophyllum buxifolium*, *Galax urceolata*, and *Gaylussacia baccata* have high constancy. On outcrops *Xerophyllum asphodeloides*, a species disjunct from the coastal plain of

Table 3. Classification of high-elevation rock outcrop communities provided by TWINSPAN. The mean cover class for plots where the species is present in the community is followed by the constancy in each community. + = present in community, but not prevalent (see text), * = regionally rare species. Species appearing in community names in bold.

Community		*Coreopsis-Schizachyrium*	*Selaginella-Carex umb.*	*Aronia-Kalmia*	*Chelone-Oxypolis*	*Paronychia-Polypodium*	*Deschampsia-Angelica*	*Picea-Leiophyl.*	*Calamagr.-Rhodod. car.*	*Aster-Menziesia*
Number of plots		15	27	11	4	23	29	16	11	18
Mean elevation (m)		1441	1395	1370	1496	1504	1734	1615	1895	1877
Homoteneity (see text)		0.467	0.475	0.550	0.644	0.584	0.502	0.567	0.643	0.569
Mean species richness (per 100 m^2)		24	16	22	26	21	19	13	13	16
Total rare species		9	8	7	12	11	17	6	9	10
MUGL	*Muhlenbergia glomerata**	+								
HELO	*Heuchera longiflora**	+								
ALCE	*Allium cernuum*	3 33								
VISA	*Viola sagittata*	2 33	+							
CABI	*Carex biltmoreana**	+	+		+					
SCSC	***Schizachyrium scoparium***	3 73	+	+		+				
COMA	***Coreopsis major***	2 80	+	2 36		+				
SOBI	*Solidago bicolor*	2 40				+				
QURU	*Quercus rubra*	2 60	+	+		+	+			
DECA	*Deschampsia cespitosa**	+					+			
CADI	*Campanula divaricata*	2 47	+			+	+			
PHOP	*Physocarpus opulifolius*	3 33				+	+			
HOCA	*Houstonia caerulea*	2 33				+				+
SOUL	*Solidago uliginosa**		+							
JUCO	*Juniperus communis* var. *depressa**		+							
ANVI	*Andropogon virginicus*		3 41	+						
SETO	***Selaginella tortipila***	+	7 93	5 36						
HOLO	*Houstonia longifolia* var. *glabra*	+	2 63	+	+		+			
DASE	*Danthonia sericea*	+	3 44	+	+		+			
DACO	*Danthonia compressa*	+	4 56	+	+		+	+		
DIAC	*Dichanthelium acuminatum*	3 67	2 70	+		+	+			
CAUM	***Carex umbellata***	3 27	2 67	+		+	+	+		
KRMO	*Krigia montana**	3 53	2 78	+	2 50	2 35	3 66		3 36	
TOGL	*Tofieldia glutinosa* ssp. *glutinosa**			+	+					
XEAS	*Xerophyllum asphodeloides*			4 45						
GABA	*Gaylussacia baccata*	+	+	4 64		+				
CLAC	*Clethra acuminata*	+	+	3 45		+				
UVPU	*Uvularia puberula*	+		2 45		+	+			
VINU	*Viburnum nudum* var. *cassinoides*	+	+	3 55	+		+			
LYQU	*Lysimachia quadrifolia*		+	2 36	+	+	+			
AMAR	*Amelanchier arborea*	+	2 44	2 82	2 75	+	+			
SOPU	*Solidago puberula*	+	2 37	2 55		+	+			
KALA	***Kalmia latifolia***	3 60	3 44	4 82	+	3 52	+	+		
ACRU	*Acer rubrum*	+	+	3 73	2 50	+	+	+		
VAPA	*Vaccinium pallidum*	3 40	+	4 45		+	+	3 50		
GAUR	*Galax urceolata*	+	+	3 64		+	+	4 50		
ARAR	***Aronia arbutifolia***	+	+	3 91		+	+	+		+
IRVE	*Iris verna*		+	3 36						
SCCA	*Scirpus cespitosus**		+	4 82	+	+	+	+	5 36	+
LIHE	*Liatris helleri**			2 55		+		+		
HUPO	*Huperzia porophila**				+					
HESP	*Heuchera* sp. 1 (sp. nov.)				4 50					
FIRU	*Filipendula rubra**				3 50					
CHOB	***Chelone obliqua***				5 100					
SACA	*Sanguisorba canadensis**	+		+	+		+			
JUAC	*Juncus acuminatus*	+			2 50					
CACR	*Carex crinita*	+			3 50					
DRRO	*Drosera rotundifolia*	+			3 50					
SOPA	*Solidago patula* var. *patula*	+	+		3 75					
OXRI	***Oxypolis rigidior***	+	+	+	3 100		+			+
ASCO	*Aster cordifolius* var. *sagittifolius*	+	+	+	3 100	+	2 41			+
HOSE	*Houstonia serpyllifolia*	+	+	+	4 100	+	2 52		+	+
THCL	*Thalictrum clavatum*	+			3 75	+				+
ATAS	*Athyrium filix-femina* ssp. *asplenioides*	+			2 75	3 74	2 62		2 45	3 39
RHMA	*Rhododendron maximum*		+		2 75	+				
HYBU	*Hypericum buckleyi**		2 30	+	4 50		+			
ARTR	*Arisaema triphyllum*				2 50	+	+			
CARU	*Carex ruthii**				3 50				+	
PAAS	*Parnassia asarifolia*				3 75				2 36	+
CHLY	*Chelone lyonii*				2 50		+			4 44
DASP	*Danthonia spicata*	3 60	2 33	+		2 74	4 55			
PAAR	***Paronychia argyrocoma***	3 60			+	3 91	+	+		
SETE	*Sedum telephioides*	2 47	+			2 65	+			+
HEVI	*Heuchera villosa*	2 33	+			2 61	3 48	+		2 61
VACO	*Vaccinium corymbosum*	4 40	4 37	+	+	4 65	3 45	+	+	+

Table 3, cont.

Community		*Coreopsis-Schizachyrium*	*Selaginella-Carex umb.*	*Aronia-Kalmia*	*Chelone-Oxypolis*	*Paronychia-Polypodium*	*Deschampsia-Angelica*	*Picea-Leiophyl.*	*Calamagr.-Rhodod. car.*	*Aster-Menziesia*
SAMI	*Saxifraga michauxii*	3 87	3 33	+	3 100	3 87	3 90	2 75	2 91	3 100
POAP	***Polypodium appalachianum***	2 40		+	+	3 78	+	2 38		2 44
HOPU	*Houstonia purpurea* var. *montana**	+				2 70	+			+
ZILE	*Zigadenus leimanthoides**		+	+		+		+		+
HUAP	*Huperzia appalachiana**			+		2 48	+		2 36	+
MIGR	*Minuartia groenlandica**					+	+			
JUTR	*Juncus trifidus**					+	+			
GERA	*Geum radiatum**					3 48	+		+	+
ARLY	*Arabis lyrata**					+				+
HYMG	*Hypericum mitchellianum/graveolens**	+			+		+		+	
DEFL	***Deschampsia flexuosa***	3 33	+		+	+	3 55			
AGPE	*Agrostis perennans*	3 40	+	+	3 50	+	3 52	+		+
DISE	*Diervilla sessilifolia*	+	3 33	+			2 45		+	
SITR	*Sibbaldiopsis tridentata*	+	+	+		3 65	4 38			
ANTR	***Angelica triquinata***	+		+		2 43	2 59	+		3 44
RUAC	*Rumex acetosella*		+			+	3 38			+
PRRO	*Prenanthes roanensis**		+				+			+
ALCR	*Alnus viridis* ssp. *crispa**						+			
RHVA	*Rhododendron vaseyi**						+	+		
BEAL	*Betula alleghaniensis*	+		+		3 48	+	2 56		+
RHCA	*Rhododendron catawbiense*	3 53	+	3 73		3 78	4 69	3 88		3 39
LEBU	***Leiophyllum buxifolium***		+	6 73			+	5 81	4 73	+
PIRU	***Picea rubens***				+		+	3 81	+	+
SOSP	*Solidago spithamaea**					+	+	3 38		+
VIMA	*Viola macloskeyi*	+			+		+	2 45		
ASMO	*Asplenium montanum*	+		+		2 35	+	+	2 36	
CAMI	*Carex misera**	+	+	+	4 50	2 65	3 41	2 50	4 100	4 89
RHCL	***Rhododendron carolinianum***		+	4 36				+	4 100	
SOGL	*Solidago glomerata*					+	3 55	+	4 64	3 61
CACA	***Calamagrostis cainii****						+	+	5 91	+
GELI	*Gentiana linearis**								2 64	
CABR	*Carex brunnescens*	+	+			+	+	+	2 38	3 44
SOAM	*Sorbus americana*	+	+	2 45		4 65	2 45	3 63	2 45	3 72
ASAC	***Aster acuminatus***			+	2 50	+	+	2 50	2 55	3 83
MEPI	***Menziesia pilosa***			+	+	3 57	+	3 56	+	3 67
VAER	*Vaccinium erythrocarpum*			+	+	4 35	+	3 44	2 36	3 44
ABFR	*Abies fraseri*			+			+	2 44	3 55	4 61
RUID	*Rubus idaeus**									+
PHCO	*Phegopteris connectilis**									+

New Jersey, occurs only in this community, but may grow in adjacent, shallow-soiled woodlands. The predominance of woody species reflects the rapid gradation into heath balds and may be related to the generally deeper soils of this community. Surrounding vegetation ranges from heath balds dominated by *Rhododendron catawbiense* to deciduous or conifer forests. At higher elevations, under otherwise similar conditions, it is replaced by the *Picea rubens-Rhododendron catawbiense* outcrop community described below.

The *Chelone obliqua-Oxypolis rigidior* wet outcrop community is a species-rich, broad-leaved herb community occurring on low-to-mid elevation (1262-1725 m) felsic outcrops with abundant seepage. It occurs on steep, lower outcrop slopes, far below the nearest summit. Sites are highly protected, shady and constantly wet. *Saxifraga michauxii*, *Aster divaricatus*, and *Houstonia serpyllifolia* are ubiquitous. On outcrops, *Chelone obliqua*, *Filipendula rubra* and *Huperzia porophila* are unique to this community, the latter two being regionally rare. The surrounding deciduous forest is dominated by *Betula alleghaniensis*, *Acer rubrum*, and *Tsuga caroliniana*, or *Picea-Abies* forest.

The *Paronychia argycoma-Polypodium appalachianum* outcrop community usually occurs at mid elevations (1347 - 1585 m) on highly exposed, SW to-NW-facing slopes, primarily over amphibolite and metabasalt, both mafic rock types (Fig. 6, below). Most occurrences are north of Grandfather Mt. *Saxifraga michauxii*, *Rhododendron catawbiense*, *Athyrium filix-femina* ssp. *asplenioides*, *Danthonia spicata*, *Houstonia purpurea* var. *montana*, *Carex misera*, *Sedum telephioides*, *Sorbus americana*, *Sibbaldiopsis tridentata*, *Vaccinium corymbosum*, and *Heuchera villosa* all have high constancy. Surrounding vegetation is usually *Quercus rubra*, with grass or heath balds less commonly as the matrix.

The *Deschampsia flexuosa-Angelica triquinata* outcrop community occurs primarily over metagabbro and metagraywacke at mid to high elevations (1650-1900 m) on SE to SW-facing slopes, or as much as 170 m lower on NW-facing slopes. The *Paronychia argycoma-Polypodium appalachianum* and *Picea rubens*, *Leiophyllum buxifolium* communities, found within the same elevation

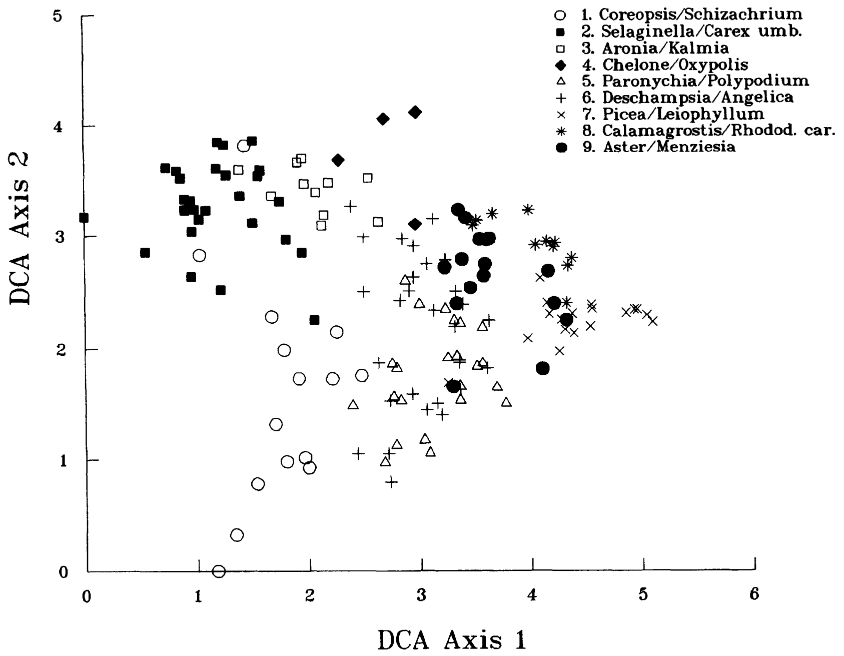

Fig. 3. DCA ordination of all 100-m^2 plots in the study area coded by the 9 TWINSPAN communities.

range, are poorly represented on these rock types. *Saxifraga michauxii*, *Rhododendron catawbiense*, *Krigia montana* and *Athyrium filix-femina* ssp. *asplenioides* have high constancy. Often the matrix vegetation is grass or shrub bald resulting from past burning and/or grazing (Gersmehl 1973; Barden 1978; Stratton & White 1982). The importance of *Angelica triquinata* may relate to its preference for balds (McLeod 1988) which could allow persistence on adjacent outcrops by a spatial mass effect (*sensu* Shmida & Ellner 1984). Exotic species are rare in the high-elevation outcrop flora, but six of the eight exotic species encountered (i.e. *Polygonum aviculare*, *Phleum pratense*, *Poa compressa*, *Rumex acetosella*, *Taraxacum officinale*, *Trifolium pratense*) either occur only in, or reach their highest constancy in this community. Presence of exotics reflects both their occurrence in surrounding grassy balds and the high potential solar radiation of these outcrops. On outcrops, *Alnus viridis* ssp. *crispa*, a regionally rare species, is unique to this community.

The *Picea rubens-Leiophyllum buxifolium* outcrop community occurs over highly fractured felsic to mafic bedrock at mid-elevations (1400-1800 m). Aspect ranges from northeast to southeast. This community is most prevalent in the Grandfather Mt. region, but also occurs in the Smoky Mts. and on the Roan Mt. massif. *Rhododendron catawbiense*, *Saxifraga michauxii* and *Sorbus americana* have high constancy. Surrounding vegetation is either heath bald or northern hardwood forest.

The *Calamagrostis cainii-Rhododendron carolinianum* outcrop community is confined to the felsic Anakeesta slate outcrops in the Great Smoky Mts. It occurs at high elevations (1650-2000 m) on steep ($\bar{x}$ = 60°), predominantly southeast or southwest-facing slopes. While soils are generally low in major cations, they are high in boron, iron, copper, and manganese, conditions more typical of soils over mafic rock. *Carex misera*, *Saxifraga michauxii*, *Leiophyllum buxifolium*, *Solidago glomerata* and *Gentiana linearis* have high constancy. *Gentiana linearis*, a species considered rare in Tennessee, occurs only on these outcrops and in other high-elevation communities nearby. *Calamagrostis cainii*, a local Southern Appalachian endemic, reaches its highest abundance and constancy here and is otherwise known from only two smaller populations on outcrops some 100 km away (Wiser 1991). Surrounding vegetation is *Picea-Abies* forest. At lower elevations under similar conditions this community is replaced by the *Picea rubens-Leiophyllum buxifolium* community.

The *Aster acuminatus-Menziesia pilosa* outcrop community usually occurs above 1700 m on the highest elevation outcrops studied (i.e. the highest summits of Grandfather Mt., Mt. Craig, Roan High Bluff, and Mt. Buckley in the Great Smoky Mts., and near the summit of Craggy Pinnacle; Fig. 7) in settings with low potential solar radiation over highly fractured bedrock. *Saxifraga michauxii*, *Carex misera*, *Sorbus americana*, *Solidago glomerata*, *Heuchera villosa* and *Abies fraseri* have high constancy. Outcrops typically occur in a *Picea-Abies* forest matrix, and the most constant species are common in these forests. With slightly lower elevation or exposure on a given mountain, this community is replaced by the *Picea rubens-Leiophyllum buxifolium* outcrop community.

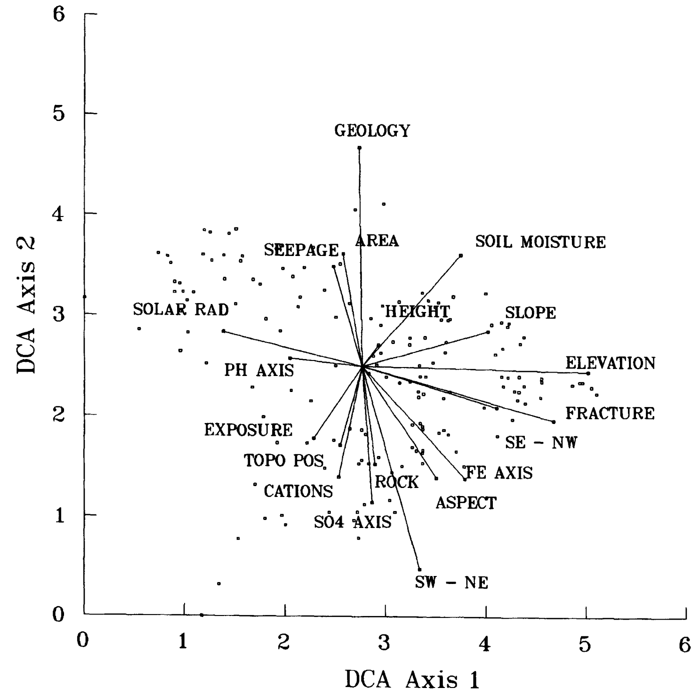

Fig. 4. Biplots of stand scores and environmental correlations for the DCA ordination of all 100-m^2 plots in the study area. Codes for environmental parameters are as in Table 4.

Comparison to previous classifications

The only previous classification of Southern Appalachian high-elevation outcrop vegetation is that of Schafale & Weakley (1990) based exclusively on subjective field evaluation. They distinguished granite dome communities (on Whiteside quartz-diorite outcrops) and high-elevation seep communities from other high-elevation cliff communities, termed high-elevation rocky summits. We similarly recognize granite dome communities (*Selaginella tortipila-Carex umbellata* community) and one type of seepage community (*Chelone obliqua-Oxypolis rigidior* community) as distinct. Schafale & Weakley pointed out that high-elevation seeps vary considerably in composition. We distribute seepage slopes across several different communities because of strong floristic similarity to nearby outcrop sites lacking seepage. Schafale & Weakley defined three geographic variants of high-elevation rocky summits. In contrast, our floristic-based classification correlates more strongly with differences in elevation, bedrock type, and surrounding vegetation composition than with geography.

Rare species

In comparison to other Southern Appalachian vegetation types, high-elevation outcrops harbor high numbers of regionally rare species (Table 3). Despite sharing a restriction to high-elevation outcrops, individual rare species vary considerably as to the type of outcrop they inhabit (Fig. 8). As a group, rare species are not confined to a particular community type or geographic region. *Geum radiatum*, *Huperzia selago*, *Solidago spithamaea*, *Prenanthes roanensis* and *Carex misera* are most frequent in the northern part of the study area, either above 1600 m on felsic or intermediate bedrock, or as much as 250 m lower on steep slopes of mafic outcrops. *Muhlenbergia glomerata* and *Deschampsia cespitosa* occur only in communities on mafic bedrock. *Carex biltmoreana*, *Solidago uliginosa*, *Hypericum buckleyi*, *Tofieldia glutinosa* ssp. *glutinosa* and *Juniperus communis* var. *depressa* generally occur south of Asheville on felsic outcrops below 1800 m. *Huperzia porophila* and *Filipendula rubra* each occurred on a single seepage slope in the *Chelone obliqua-Oxypolis rigidior* community. *Scirpus cespitosus* and *Liatris helleri* occur up to 1990 m and 1620 m respectively and descend to elevations below those studied (Alan Weakley pers. comm.). Although both species occur on mafic sites, they are most abundant and constant on felsic bedrock in the *Aronia arbutifolia-Kalmia latifolia* community.

Soil properties

The outcrop soils were highly organic with low pH ($\bar{x}$ organic matter content = 31%, $\bar{x}$ pH = 4.1). That pH has low loadings until the fourth PCA axis suggests that pH is not a strong indicator of soil nutrient status in these soils. The positive correlation between pH and aluminum

Fig. 5. A geographic outlier of the *Selaginella tortipila-Carex umbellata* outcrop community on Hawksbill Mountain, Linville Gorge, North Carolina. At these elevations *Pinus pungens* and *P. rigida* dominate adjacent forests. Dense *Selaginella* mats, such as pictured here, are rare in nearby areas owing to abrasion from hikers and rock climbers.

Fig. 6. This example of the *Paronychia argycoma-Polypodium appalachianum* outcrop community occurs on Bluff Mt. in Northwestern North Carolina. *Saxifraga michauxii*, widespread on outcrop communities, is flowering in the foreground.

Fig. 7. Outcrop communities at the highest elevations (1700 m+) usually occur on highly fractured bedrock on highly exposed sites as shown here on Grandfather Mountain, North Carolina. The surrounding forest is *Picea-Abies*. On the steepest slopes, herbaceous species persist in only a few cracks and crevices.

also is contrary to conventional wisdom (Brady 1984). This correlation holds even when organic matter influence is removed through partial correlation, or unusually high or low aluminum soils are excluded from analysis.

Perennial seepage occurred on 28 100-m^2 plots over a range of bedrock types. Seepage slopes tend to occur farther below summits than do outcrops without seepage ($\bar{x}$ = 103 m below summit vs. 38 m below summit for non-seepage slopes); $p < 0.0001$ by *t*-tests). Seepage presence relates to rock permeability, the strike and dip of metamorphic foliation or outcrop fractures, and topographic influences on sub-surface flow (Boorman & Platt 1958; Schafale & Weakley 1990). Ground water tends to follow rock formations on mountain slopes and moist habitats often develop on and near downslope outcrops (Hursh & Haasis 1931). Soils from 100-m^2 plots with seepage have higher water holding capacity, pH, and sodium and lower sulfate than do those lacking seepage (all $p < 0.01$ by t-tests).

Over a 100-m^2 plot, seepage presence is rarely, if ever, uniform. In 100-m^2 plots with seepage, individual 1-m^2 subplots with seepage tend to have steeper slopes ($\bar{x}$ = 42° vs. 34°; $p = 0.007$ by a *t*-test), higher pH, sodium, manganese, and lower phosphorus than do non-seepage microhabitats (all $p < 0.01$ by *t*-tests). These differences are probably a consequence of transport of cations leached from higher rocks and soils.

On 100-m^2 plots lacking seepage, significant, but small soil differences are apparent on mafic (43 plots) vs. felsic rock (55 plots). Boron, copper and phosphorus are higher, and sodium is lower in soils over mafic rock than in those over felsic rock (all $p < 0.01$ by a *t*-test, Fig. 4). Similar patterns emerge for 1-m^2 subplots.

As soil pH and cations are usually elevated in soils over mafic rock elsewhere, the lack of strong differences between mafic and felsic bedrock in magnesium, manganese and pH and only small differences in calcium are surprising. Nonetheless, nine of the 12 plots with the highest loadings on the cations axis occur on mafic rock or on rock with occasional mafic veins; the remaining three plots high in cations are on seepage slopes over felsic rock. Soils formed over metabasalt, a mafic rock, may differ in nutrients with slope position (Rohrer 1983). Non-ridgetop soils retain moisture and nutrients and have high relative amounts of phosphorus, potassium, calcium, magnesium and manganese, whereas ridgetop soils are thin, moisture quickly evaporates, and downslope leaching results in only intermediate levels of these nutrients (Rohrer 1983).

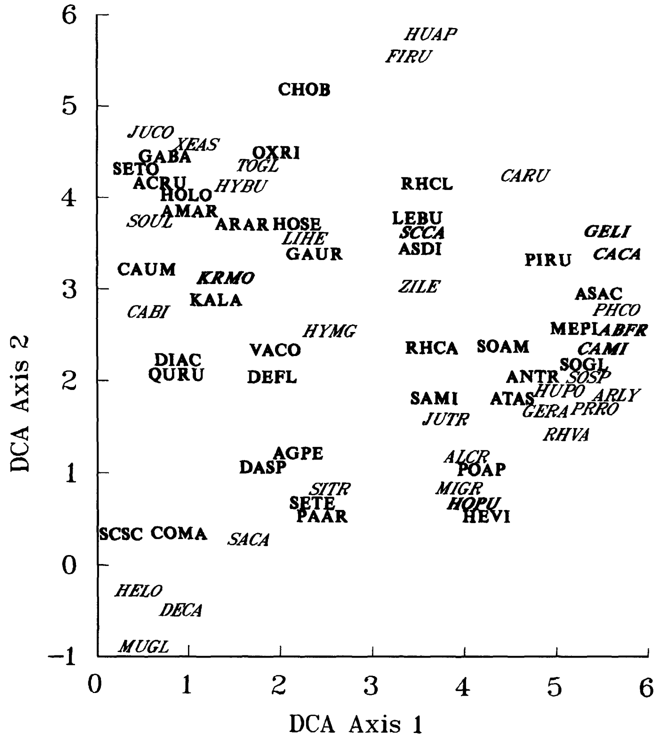

Fig. 8. Species scores for a) species with high constancy mentioned in community descriptions (bold) and b) regionally rare species (as defined by the North Carolina or Tennessee Heritage Programs; italics). Regionally rare species with high constancy are in bold italics. Species codes are provided in Table 3.

Scale and relationships between composition and environment

Across the Southern Appalachian region, the environmental variables that correlate with floristic composition of the 100-m^2 plots are many and their patterns complex (Fig. 4, Table 4); similar DCA eigenvalues across the first three axes suggest highly multidimensional data. The first DCA axis correlates most strongly with elevation and fracture index and moderately with potential solar radiation, aspect and SE-NW location (Fig. 4, Table 4). These correlations suggest that this DCA axis corresponds to a complex temperature-moisture gradient from hot, dry sites to cool, moist ones. DCA axis 2 correlates strongly with mafic vs. felsic bedrock and SW-NE location, and moderately with the iron and sulfate soil axes (Fig. 4, Table 4). Mafic bedrock predominates in the northeast portion of the study area and diminishes in prominence to the southwest.

Within each bedrock type except Whiteside quartz diorite, vegetation relates strongly to elevation (Table 4) with the strength of this relationship corresponding to the elevation span sampled. When this span is low (<500 m, i.e. amphibolite, metagabbro, Anakeesta slate), the dominant vegetation gradient relates more strongly to potential solar radiation. The relationship between vegetation composition and soil attributes varies among bedrock types. However, the importance of some soil variables may be a consequence of long gradients or extreme values for the particular nutrient. In particular, the significance of the pH and cations axes on amphibolite and the sulfate axis on meta-arkose may result from long gradients, whereas extreme soil values may be important in the case of the sulfate axis on metagabbro. Other parameters strongly correlated with 100-m^2 scale composition on individual bedrock types are slope (amphibolite and metagabbro), exposure (Anakeesta slate), fracturing index (metagraywacke and Whiteside quartz diorite), and percent rock, outcrop height and area, and aspect (metagraywacke) (Table 4).

For 1-m^2 subplots on metagabbro, meta-arkose, Anakeesta slate, and metagraywacke, DCA axis 1 scores correlate highly (Pearson's $r > 0.80$; $p < 0.0001$) with corresponding 100-m^2 DCA axis 1 scores. In contrast, over amphibolite DCA axis 2 of the 1-m^2 subplots surpasses axis 1 in correlation strength with 100-m^2 plot DCA axis 1 scores ($r = 0.73$, $p < 0.0001$), revealing a primary compositional gradient at this scale distinct from that represented by variation among 100-m^2 plots. Over Whiteside quartz diorite, gradient structure also differs for 1-m^2 subplots as their scores are only moderately correlated ($r < 0.53$) with the respective 100-m^2 plot scores.

After removal of the influence of 100 m^2 variation, soil depth, percent exposed bedrock, maximum vegetation height and soil chemistry (cations, pH, and sulfate axes) are highly correlated with compositional variation among all 596 1-m^2 subplots (Table 4). As expected,

Table 4. Correlations between site parameters and DCA axes for both plot sizes at the large geographic extent of the entire study area and smaller geographic extent of individual bedrock types. Significance levels are indicated as: * = $p \leq 0.05$; **= $p \leq 0.01$; *** = $p \leq 0.001$; **** = $p \leq 0.0001$. When significant correlations are many, only those with $p \leq 0.0001$ are shown. fracture = rock fracturing index; solrad = potential solar radiation; sw-ne, se-nw, = relative long and short geographic axes of the mountains, respectively; geology = index from 1 to 3 indicating broad geologic categories (i.e. 1 = mafic, 2 = intermediate, 3 = felsic); area = outcrop area category; height = outcrop vertical relief category; topopos = topographic position index; exposure = exposure index; rock = % exposed bedrock; depth = soil depth; maxveght = maximum vegetation height; moss = % cover of moss; baresoil = % cover of bare soil; shade = % sky obstructed; seepage, dir ppt, drip, runoff = 1 for presence of seepage, direct precipitation, drip from above or runoff as moisture sources, 0 for absence; soilmoist = soil moisture holding capacity; PCA soil axes names are as in Table 2.

	100-m^2 plots				1-m^2 subplots with 100 m^2 scores partialed out			
	DCA Axis 1		DCA Axis 2		DCA Axis 1		DCA Axis 2	
Bedrock type	Var.	Corr. coeff.	Var.	Corr. coeff.	Var.	Corr. coeff.	Var.	Corr. coeff.
ALL BEDROCK TYPES	elevation	0.7614****	geology	0.7131****	sulfate axis	– 0.2107****	cations	0.3506****
n = 154 (100m^2)	fracture	0.6839****	sw-ne	– 0.6925****	depth	0.2234****	maxveght	0.3147****
n= 596 (1m^2)	solrad	– 0.4591****	iron axis	– 0.3874****	rock	– 0.1815****	rock	– 0.1590****
	se-nw	0.4759****	sulfate axis	– 0.4919****	slope	– 0.1208**	ph axis	0.1871****
	slope	0.3952****	area	0.3806****			depth	0.1549****
	iron axis	0.3973****	eepage	0.3455****			dir ppt	0.1608****
	sw-ne	0.3111****	aspect	– 0.3329****			drip	– 0.1318**
			cations	– 0.3035****			moss	– 0.1303**
			rock	– 0.3021****			seepage	0.1279**
AMPHIBOLITE	slope	– 0.8433****	elevation	0.7040****	rock	0.3374***	sulfate axis	– 0.3701****
n = 27	solrad	0.6092***			runoff	0.2701**		
n = 108	iron axis	– 0.5013**			depth	– 0.2529**		
	ph axis	0.5087**			maxveght	– 0.2860**		
	cations	0.4754*						
METAGABBRO	sulfate axis	0.9283****	elevation	– 0.8199***	cations	.4104***	none sig.	
n = 13	slope	– 0.7481**			rock	– 0.3822**		
n = 49	solrad	0.7372**			maxveght	– 0.3570*		
					shade	– 0.2905*		
META-ARKOSE	elevation	– 0.8533****	soilmoist	– 0.5677**	iron axis	0.4190****	depth	0.3138**
n = 25	sulfate axis	– 0.5934**			topopos	0.3592***	rock	– 0.2974**
n = 94					depth	0.2475*	dir ppt	0.4043****
							shade	– 0.2951**
							drip	– 0.2697**
METAGRAYWACKE	elevation	– 0.9483****	height	0.6376**	sulfate axis	– 0.5425****	runoff	0.2331*
n = 19	fracture	– 0.6098**	slope	0.5439*	depth	0.3414**		
n = 78	rock	0.5471*	cations	– 0.5183*	slope	– 0.3065**		
	area	– 0.5372*	fracture	0.5330*	rock	– 0.2796*		
	sulfate axis	0.5317*						
	rock	0.4847*						
	ph axis	0.4662*						
ANAKEESTA SLATE	cations	0.8096**	exposure	– 0.6650*	baresoil	0.3966*	none sig.	
n = 10	solrad	– 0.7415*						
n = 30	elevation	0.7267*						
WHITESIDE QUARTZ DIORITE	iron axis	0.7429***	solrad	0.5063*	depth	– 0.4220***	ph axis	– 0.4411***
n = 17	fracture	0.6201**			sulfate axis	0.3643**	moss	– 0.3254**
n = 66	slope	0.5246*			runoff	0.3357**	soilmoist	– 0.2894*
					rock	0.3264**		
					shade	– 0.3814***		
					exposure	0.3306**		

soil depth is strongly correlated with percent exposed bedrock; hereafter their covariation is discussed as one complex soil depth gradient.

Among 1-m^2 subplots on individual bedrock types, the soil depth gradient is strongly correlated with compositional variation over amphibolite, meta-arkose, metagraywacke and Whiteside quartz diorite (Table 4). In contrast, over metagabbro maximum vegetation height and shade relate more strongly to composition than does soil depth, and over Anakeesta slate only the amount of bare soil present relates to composition.

Among 100-m^2 plots on a bedrock type, total inertia is three to four times lower than for the entire data set, in part due to decreased sample sizes. Reducing geologic, and as a result geographic, variation in the data reduces dimensionality and thus total inertia. Measured site parameters account for 78 - 93 % of compositional variation vs. 27 % at the larger geographic extent.

For 1-m^2 subplots, both across the region and within bedrock types, total inertia is two to three times greater than for 100-m^2 plots. For subplots, site parameters account for less compositional variation and are more weakly correlated with the ordination axes. Across the study area, 4 % of the compositional variation among 1-m^2 subplots is due to compositional differences among the 100-m^2 plots to which they belong (Table 5). Within each of the six bedrock types, variation among the 100-m^2 plots accounts for 7 - 10 % of the variation among 1-m^2 subplots (Table 5). After partialling out the 100-m^2 plot score, measured site parameters account for an additional 7 % of compositional variation among all 1-m^2 subplots and from 14 - 23% of the remaining compositional variation within bedrock types. Across the study area, 87 % of the compositional variation among 1-m^2 subplots is explained by neither 100-m^2 plot scores or measured site parameters. Within bedrock types this decreases to 49 - 74 %.

Discussion

Variation in gradients at different scales

Observational scale, both spatial extent and plot size, influence detection of compositional variation and ecological pattern (e.g. Allen & Starr 1982; Meentemeyer & Box 1987; O'Neill 1988; Wiens 1989; Reed et al. 1993). Large extents may be required to detect subtle, geographic gradients in species composition. Plot size can influence which environmental variables are useful in predicting composition as well as the degree to which plant-plant interactions obscure environmental determinism (Reed et al. 1993).

Reed et al. (1993) found predictability of composition from site parameters to decrease with increased spatial extent and suggested that this reflects more complex gradient structure and increased interactions between site parameters. Higher total inertia and reduced ability of site parameters to account for compositional variation across all Southern Appalachian outcrops, as opposed to within bedrock types, likely reflects similar complex gradient structure and is consistent with Reed et al's interpretation. Across outcrops, geologic and geomorphic complexity increase with increased extent. At the regional extent, climatic variation, disturbance, and historical influences (cf. van der Maarel et al. 1987) further reduce the ability of measured site parameters to explain compositional variation, although bedrock differences override climatic variation in plant communities elsewhere (Orlóci & Stanek 1979; Kirkpatrick 1982). Higher total inertia may also reflect the larger sample size when all bedrock types are combined.

Despite considerable environmental variation, particularly in geology and climate, there are consistent compositional patterns, both regionally and on most bedrock types. Elevation and potential solar radiation relate strongly to composition, both within and among bedrock types. The sulfate and iron PCA soil axes are both important across the region. Within bedrock types the former is important over bedrock types that ascend to higher elevations, whereas the latter is important on the two bedrock types occurring predominantly at lower elevations. The soil depth gradient is important across most bedrock types.

On different bedrock types or on north vs. south slopes, 1-m^2 subplots may differ because of these overall site contrasts as well as because of microhabitat differences. Among 100-m^2 plots with similar site conditions, subplot differences due to microhabitat should become more apparent. Accordingly, within a bedrock type, variation among 100-m^2 plots accounts for less of the variation among 1-m^2 subplots than among bedrock types (Table 5). Similar observations have been made in saxicolous lichen communities, where parameters such as overall slope, aspect, and altitude determine species distribution patterns within rockfaces in conjunction with microsite factors (John & Dale 1990), and along the Niagara escarpment, although microsite position had the largest influence there (Larson et al. 1989).

A reduced correlation between vegetation composition and environment at smaller plot sizes was also observed by Reed et al. (1993). On the outcrops this may be caused by (1) increased importance of plant-plant interactions on smaller subplots (Kershaw & Looney 1985; Reed et al. 1993), (2) increased variance due to small sample size and the associated variation in sample composition (Reed et al. 1993), or (3) competition for regeneration sites. At a small scale, plant-plant interactions are important on Southeastern piedmont outcrops (Sharitz & McCormick 1973; Meyer et al. 1975), but competition and niche differentiation may be unimportant in limestone pavement communities of Britain (Silvertown 1983).

After 100-m^2 plot variation is partitioned out, the environmental variables that correlate with composition at the 1-m^2 scale are generally different from those important at 100 m^2. This agrees with Reed et al. (1993) and Castro et al. (1986) who found different predictive parameters for different size plots. While slope and potential solar radiation are important region-wide and within certain bedrock types on 100-m^2 plots, they are rarely correlated with variation among 1-m^2 subplots (although they do vary at this scale). The relative importance of soil variables also differ between plot sizes.

Gradient comparisons among bedrock types

The consistent relationships of elevation, potential solar radiation and aspect to composition across bedrock types echoes the general importance of these gradients for Southern Appalachian community composition. Elevation, a complex gradient that parallels temperature, moisture, and soils gradients, is usually a dominant environmental correlate with vegetation in mountainous terrain, including the Southern Appalachians (e.g. Whittaker 1956; Day & Monk 1974; Lindsay & Bratton 1979; Golden 1981; Callaway et al. 1987; McLeod 1988). Further, maximum elevation in a range may have influenced high-elevation species persistence during the warmest postglacial times (Whittaker 1956; White et al. 1984; White & Miller 1988). The second major outcrop gradient corresponds to topographic/moisture gradients, generally described via indices derived from topographic position, aspect, or exposure (Whittaker 1956; Day & Monk 1974; Callaway et al. 1987), or measures of potential solar radiation and aspect (Lindsay & Bratton 1979; McLeod 1988).

In mountain forests, soil variation is often closely linked with aspect, slope and topographic position (Mowbray & Oosting 1968; Jenny 1980; c.f. Allen & Peet 1990). In this study, compositional relationships with soil were found to change with geology, but no consistent relationships with aspect, slope and topographic position were found. Geology influences soil chemistry and drainage as well as correlations with slope position. Analogous inconsistencies in correlations of slope position and aspect with Southern Appalachian forest soil properties have been found between soils derived from granitic biotite gneiss and those from highly siliceous sandstone and siltstone (Losche et al. 1970).

Comparisons with patterns on other outcrops

On outcrops elsewhere, small-scale compositional variation most often relates to soil depth/soil moisture gradients typically considered to represent successional sequences (e.g. Oosting & Anderson 1937, 1939; Quarterman 1950; Burbanck & Platt 1964; Sharitz & McCormick 1973; Silvertown 1983; Ohsawa & Yamane 1988; Collins et al. 1989). The importance of the soil depth gradient here agrees with these findings.

Previous comparisons of vegetation on outcrops of different bedrock types have attributed differences to geology (Ware 1990; Fuls et al. 1992), disturbance (Fuls et al. 1992), and combinations of moisture, aspect and slope (Fuls et al. 1992). Compositional variation among outcrop sites on particular bedrock types has been attributed to differences in elevation (Ashton & Webb 1977; Maycock & Fahselt 1992), solar radiation, slope, aspect, or exposure (Winterringer & Vestal 1956; Ashton & Webb 1977; Whitney & Moeller 1982; Makirinta 1985), moisture (Maycock & Fahselt 1992), degree of shading (e.g. Quarterman 1950), substrate texture (Burgman 1987; Maycock & Fahselt 1992), geographic position (Burgman 1987) and soil chemistry (Jarvis 1974; Mäkirinta 1985). In Southern Appalachian outcrops, strong relationships between composition and elevation, slope, aspect and related parameters, both within and among bedrock types, resemble patterns on outcrops in other mountainous localities or areas of high relief (e.g. Winterringer & Vestal 1956; Ashton & Webb 1977; Whitney & Moeller 1982; Maycock & Fahselt 1992; John & Dale 1990). This contrasts with results from outcrops which occur in localities lacking strong local relief such as those of the nearby Southeastern piedmont where such parameters are weakly, if at all, related to composition.

As insular habitats, outcrops are rare in the landscape and determination of general patterns between composition and environment may require study over a wide geographic range. However, study of vegetation

Table 5. Percentages of variation of species composition on 1-m^2 subplots accounted for by (1) variation among 100-m^2 plots, (2) site parameters measured for 1-m^2 subplots, (3) variation shared between the two plot sizes. Based on partial CCA analyses.

	% of variation explained			
	100-m^2 stand scores	Microenvironment	100-m^2 stand scores + microenvironment	Total
Complete data set	3.6	7.3	2.2	13.1
Amphibolite	8.8	14.0	3.5	26.3
Metagabbro	13.2	22.7	6.7	42.6
Meta-arkose	8.8	17.0	5.1	30.9
Whiteside quartz-diorite	8.8	19.3	4.6	32.7
Metagraywacke	11.5	14.4	3.9	29.8
Anakeesta Slate	19.0	19.4	12.8	51.2

over a wide geographic extent may result in geographic variation induced by either dispersal limitation or large-scale environmental shifts obscuring patterns that are clear and consistent at smaller scales. Owing to their rarity and isolation, insular habitats have discontinuous distributions along environmental gradients. Thus, differences between locations may be pronounced and consistent microscale patterns may be obscured. Our study provides an approach to overcome some of these problems. We overcame the obscuring influence of large-scale geologic variation by partitioning our data by bedrock type. In other localities or on other types of habitat islands useful partitions might be geographic position or elevation (e.g. Peet 1981). The application of partial ordination allowed us to segregate aspects of small-scale ($1 \mathrm{m}^2$) pattern into those related to site ($100 \mathrm{m}^2$) differences and those related to microhabitat ($1 \mathrm{m}^2$). Strong spatial autocorrelation of composition of insular habitats has important conservation implications. For the outcrops, a reserve strategy must include sites from both a range of bedrock types and a range of geographic locations to be sufficiently representative. Study of vegetation of insular habitats by use of samples collected at multiple scales over wide geographic ranges, together with strategic application of analytical techniques offers an opportunity to continue to advance our knowledge and understanding of how environmental factors and dispersal processes combine to determine the distribution and abundance of plant species of insular vegetation.

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