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GEOGRAPHIC VARIATION IN FOREST DISTRIBUTION ACROSS FIVE LANDSCAPES IN THE SOUTHERN APPALACHIAN MOUNTAINS OF NORTH AND SOUTH CAROLINA

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ABSTRACT.—Vegetation plot data from five Southern Appalachian landscapes, including the Black and Craggy Mountains, Ellicott Rock Wilderness, Linville Gorge Wilderness, Shining Rock Wilderness and the Thompson River Gorge were used to examine geographic variation in forest composition. The 647 plots were divided into three nutrient classes based on available manganese levels (low-, mid- and high-nutrients). Six regional vegetation classes were identified using Ward's clustering method. Geographic variation in forest distribution was examined by comparing the distribution of vegetation classes along standard elevation and topographic-moisture gradients within each of the three nutrient regimes for each landscape. Although vegetation observed in the two high-elevation landscapes (the Black and Craggy Mountains, Shining Rock Wilderness) were consistent with Whittaker's (1956) model of Great Smoky Mountain vegetation in that elevation and topographic-moisture were strongly correlated gradients, soil nutrient status was found to be equally important. Vegetation in the three low-elevation landscapes was also strongly correlated with soil nutrient status and topographic-moisture, but the relationship with elevation was weaker. Individual vegetation classes exhibited different responses to soil nutrient status, elevation and topographic position across the five landscapes. Variability in the association with and position on these gradients of vegetation classes results from the complex interplay of climate, geology, topographic complexity, land-use history and the natural disturbance regime.

KEYWORDS.—Cove forest, elevation, forest, geographic variation, landscape, manganese, *Pinus*, *Quercus*, soil nutrients, Southern Appalachian Mountains, topographic-moisture, *Tsuga*, vegetation.

For forty years ecological and botanical studies within the Southern Appalachian region have used Whittaker's (1956) analysis on the vegetation of the Great Smoky Mountains as the model for understanding landscape-scale variation in plant species distributions. Whittaker (1956) suggested that vegetation was primarily distributed along elevation and topographic-moisture gradients, and most subsequent studies of Southern Appalachian vegetation (e.g., Ramseur, 1960; Golden, 1981; McLeod, 1988) have reiterated the primary importance of elevation and topographic position or moisture as factors controlling forest composition. Some subsequent workers (McLeod, 1988; Patterson, 1994; Newell, 1997; Newell and Peet, 1998) have identified soil nutrient status as a third gradient critical for understanding vegetation patterns in this region. Moreover, despite the fact that vegetation-environment relationships are well known for a few individual landscapes within this region, little is known of how such gradient relationships vary geographically. Although the elevation and topographic-moisture gradients employed by Whittaker and others are of considerable heuristic value, they are complex, composite gradients that do not necessarily vary in a consistent fashion with the environmental and resource gradients to which plants respond (Austin and Cunningham, 1981). Consequently, there is little reason to expect that the patterns observed by Whittaker (1956) are consistent across the region.

Differences in community distribution between specific locations within the Southern Appalachian Mountains are little known. In contrast to the comparative wealth of literature describing vegetation communities within individual landscapes, only a few studies have examined regional distributional patterns of specific individual species or community types across the Southern Appalachian Mountain region (e.g., Mark, 1958; Zobel, 1969; DeLapp, 1978; White and Cogbill, 1992; Wiser et al., 1996). This not only limits our ability to place landscape-level vegetation studies within a regional context, but also our ability to consider the region from a broader geographical perspective. Geographic variation in species distribution can be measured by comparing the distributions of species and communities along consistent environmental gradients such as elevation and topographic position (see

Allen et al., 1991). The primary objective of this study was to quantify geographic variation within forest vegetation of the Southern Appalachian Mountains of North and South Carolina with the aim of determining how forests change geographically and with respect to consistent gradients of elevation, topographic-moisture and soil fertility. In particular, we sought to determine whether particular forest communities occur under the same environmental conditions at all localities, and if not, whether shifts in community distribution with respect to elevation and topographic position correspond to a simple latitudinal gradient.

STUDY AREAS

Data from five landscapes between 3,500 and 35,000 hectares in size, are used in this study (Figure 1): the Black and Craggy Mountains (hereafter Black Mountains), Ellicott Rock Wilderness (Ellicott Rock), Linville Gorge Wilderness (Linville Gorge), Shining Rock Wilderness (Shining Rock) and the Thompson River Gorge (Thompson River). These localities lie within the Blue Ridge Physiographic Province which consists of a series of resistant, metamorphosed Precambrian thrust sheets which overlay younger basement rocks (Horton and Zullo, 1991). Linville Gorge, located in Burke County, represents the drier, lower-elevation regions on the eastern edge of the Mountains and spans an elevation range from 400 to 1250 m. The study area consists of a long, narrow, rugged valley dominated by highly dissected slopes (Newell and Peet, 1998). The Black Mountains and Shining Rock represent two of the high-mountain landscapes within the Southern Appalachian Mountains (Ramseur, 1960). Shining Rock, ranging in elevation from 970 to 1800 m, is centrally located in the Balsam Mountains of Haywood County (Newell, 1997). Further north in Yancey and Buncombe Counties, the Black and Craggy Mountains span an elevational range from 730 m to the top of Mount Mitchell at 2040 m (the highest point in eastern North America; McLeod, 1988). Ellicott Rock and Thompson River, located astride the junction of North and South Carolina, represent the low-elevation, high-rainfall Southern Escarpment Region of the Southern Appalachian Mountains. Elevations range from 600 to 1130 m at Ellicott Rock and from 335 to 1340 m at Thompson River. Both areas are complex landscapes of broad ridges, sideslopes and coves (Wentworth, 1980; Patterson, 1994).

Annual rainfall levels vary across the Southern Blue Ridge Region from a low of about 1000 mm per year in the Asheville Basin to about 2500 mm

GEOGRAPHIC VARIATION IN FOREST DISTRIBUTION

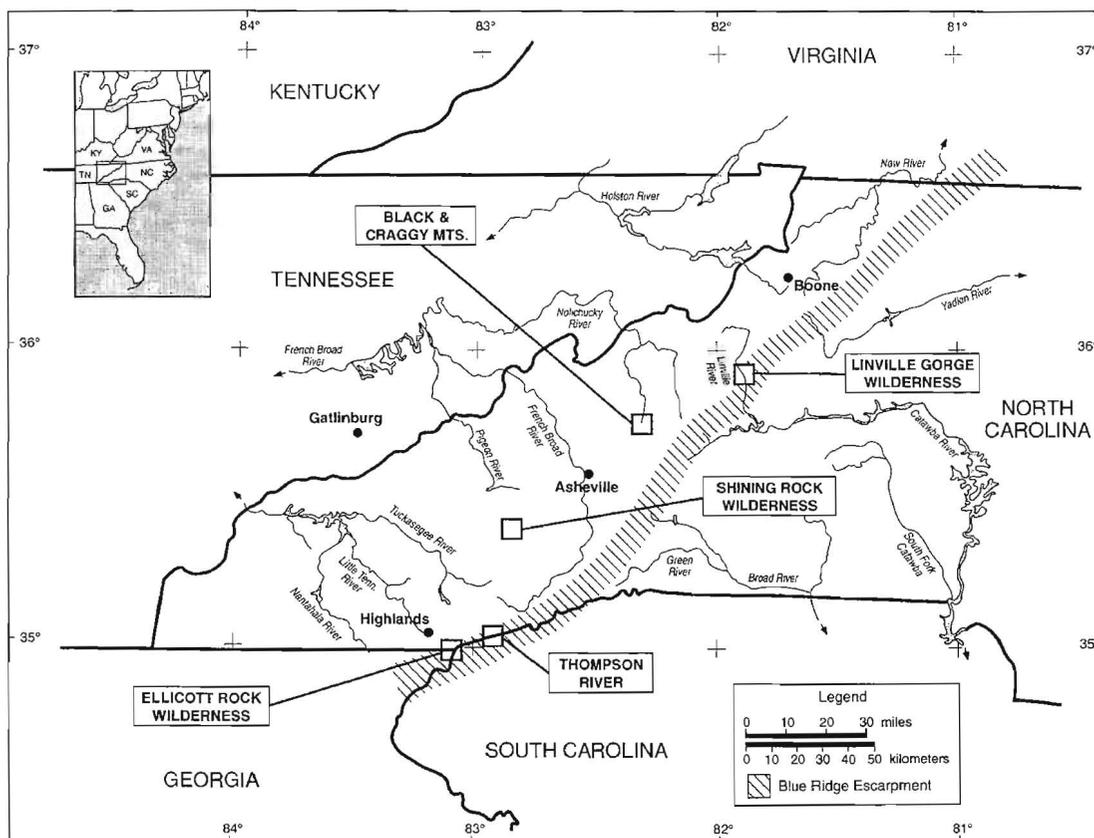


Figure 1.—Map of the Southern Appalachians of the North Carolina showing the locations of the five landscapes included in this study.

along the southern escarpment. Rainfall in the Linville Gorge vicinity ranges from 1250 mm at Banner Elk, 26 kilometers (km) north of Linville Gorge to 1625 mm at Blowing Rock, 31 km north-east of Linville Gorge. There is a rainfall gradient across the Shining Rock region from 1825 mm, 7 km south-east at the Pink Beds on the front-face of the high-rainfall escarpment, to 1025 mm 19 km north at Canton, in the rain shadow area associated with the Asheville Basin (Earthinfo Inc., 1989). Rainfall in the Black Mountains area ranges from 1170 mm to 1870 mm (McLeod, 1988). Ellicott Rock averages approximately 2100 mm of rain per year (DuMond, 1970), while records from gorges adjacent to Thompson River suggest a mean annual rainfall of between 2300 and 2500 mm for the wetter, upper-gorge region (Wentworth, 1980).

Rock-types underlying the five landscapes differ. Linville Gorge lies within the Grandfather Mountain Window where relatively younger, but still Precambrian rock shows through the ancient overthrust rocks of the Blue Ridge. This locality is underlain by a combination of quartzite, meta-arkose, phyllite and gneiss (D'Agostino et al.,

1986). Shining Rock contains highly metamorphosed sedimentary rocks (Hadley and Nelson, 1971; Butler, 1973) which are predominantly Precambrian mica gneiss and garnet-mica schist, with Paleozoic migmatite also present (Lesure, 1981). The Black Mountains are mainly underlain by mica-garnet schist, with layers of quartz-biotite gneiss and meta-arkose, but lenses of hornblende-gneiss or amphibolite also present (Howell, 1974; Lesure et al., 1982). Ellicott Rock is underlain by a variety of rock types, including amphibolite, granitic metagreywacke, biotite muscovite schist, aluminous garnet schist, and gneiss (Bell and Luce, 1983; Luce et al., 1983). The Thompson River region consists of a mix of Precambrian and lower Paleozoic igneous and metamorphosed rocks (Stuckey, 1965).

Ellicott Rock, Shining Rock and Thompson River, and areas within the Black Mountains were extensively logged in the early twentieth century and were subsequently impacted by intense fire. In contrast, Linville Gorge and areas within the Black Mountains contain primarily old-growth forests.

MATERIALS AND METHODS

Field Sampling

This study is based on 647 vegetation plots (141 from the Black Mountains, 54 from Ellicott Rock, 159 from Linville Gorge, 143 from Shining Rock, 150 from Thompson River; see Newell, 1997; McLeod, 1988; Newell and Peet, 1998; Patterson, 1994; Wentworth, 1980, respectively, for detailed discussions of the vegetation at these localities). Plots were located across the range of available elevations and topographic and geologic conditions so as to capture the topographic and edaphic diversity present at each locality. Each plot was located in an area of comparatively homogeneous vegetation and topography.

For Ellicott Rock, Linville Gorge and Shining Rock, the standard recording unit consisted of contiguous 0.01 ha (10 x 10 m) modules (typically ten, but a smaller number where the spatial extent of homogeneous vegetation or topography could not accommodate a full 0.1 ha). Cover of each vascular species was estimated for each of four intensively sampled modules in an aggregate plot using a standard ten-class system: 1=trace, 2=0-1% cover, 3=1-2%, 4=2-5%, 5=5-10%, 6=10-25%, 7=25-50%, 8=50-75%, 9=75-95%, 10=95-100%. If the full aggregate plot contained 4 or fewer modules all modules were measured intensively. Presence and cover were estimated for any additional species present in the remaining (usually 6) modules. Overall plot mean cover for each species was estimated by converting cover classes to their respective midpoint percentage value, averaging these across the entire plot aggregate and then converting percentages back to cover classes (see Patterson, 1994; Newell, 1997; Newell and Peet, 1998, Peet et al., 1998). At the Black Mountains and Thompson River vegetation was sampled with 0.1 hectare plots similar to those used by Whittaker (1960) and Peet (1981). At the Black Mountains leaf cover of all species was estimated using a modified seven-class Braun Blanquet scale; these values were subsequently converted to the standard ten-class system described above. Absolute percentage cover values for leaf area of species <1.4 m tall at Thompson River were similarly converted to the standard ten-class scale. Woody species were recorded by stem diameter at breast height (1.4 m) at Thompson River and were converted to the ten-class cover scale by regression methods using cover data from Ellicott Rock.

Botanical nomenclature follows Kartesz (1994), except that *Quercus montana* is accepted in preference to *Q. prinus*.

Elevation, slope and aspect were recorded for each plot. Potential direct beam solar irradiation was calculated from slope, aspect and latitude using the tables of Frank and Lee (1966). Site topographic position (five-point scale from valley bottom to ridgetop) and slope curvature (five-point scale from concave to convex; see Parker, 1982) were determined from 1:24,000-scale topographic maps by characterizing these features within a cell of approximately 125 m diameter around the plot.

Four soil samples were collected from the top 0.1 m of soil below the litter layer in most plots (see Figure 2). Total exchange capacity, pH, percent humic matter, extractable P, exchangeable cations (Ca, Mg, K, Na), percentage base saturation, extractable micro-nutrients (B, Fe, Mn, Cu, Zn, Al) and soluble sulphur were determined for each subsample. The Mehlich III method was used for nutrient extractions (Mehlich, 1984) and percentage humic matter was determined by loss on ignition. Chemical analyses were conducted by Brookside Laboratories, Inc., New Knoxville, Ohio (for Ellicott Rock, Linville Gorge, Shining Rock) or the North Carolina State Soil Testing Laboratory, Raleigh, North Carolina (for Black Mountains, Thompson River). All soil values for a plot (typically four) were averaged to obtain a single plot value for each variable. Compatible soil information was not available for 59 plots at Thompson River and 32 at the Black Mountains (see Figure 2).

Data Analysis

The influence of topography on forest distribution has been quantified in numerous studies throughout the Southern Appalachian Mountains (e.g., Whittaker, 1956; Callaway et al., 1987; McLeod, 1988; McNab, 1993; Fels, 1994; Patterson, 1994; Newell, 1997; Newell and Peet, 1998). Specific topographic components such as slope position, curvature, orientation and solar radiation strongly influence factors such as site moisture (Selby, 1985), and in this study these components were used to develop a topographic moisture index (TMI) using a modified version of Parker's (1982) topographic relative moisture index. Following Parker (1982), TMI values range from 0 to 60, but we reversed the scale to facilitate direct comparisons with previous graphical models of Southern Appalachian vegetation (e.g., Whittaker, 1956; McLeod, 1988) where higher index values correspond to increasingly xeric conditions. TMI is an additive scalar based on the summed influence of three topographic characteristics. Topographic position (valley bottom = 0, ridgetop = 20) was assigned

on a twenty-point scale and slope curvature (concave both across and upslope = 0, convex = 10) was assigned a ten-point scale following Parker (1982). While Parker's (1982) index used slope aspect and slope steepness as separate characteristics of his model, we combined these by using potential direct beam solar irradiation (Frank and Lee 1966). Solar radiation values ranged from 0.19 to 0.61 and these were rescaled to range between 0 and 30.

A standard gradient representation was established to facilitate between-landscape comparisons of landscape-specific vegetation composition with respect to major environmental factors. Gradient diagrams have been used to summarize vegetation-environment relationships along elevation and topographic-moisture gradients in many individual landscape-level studies (e.g., Whittaker, 1956; McLeod, 1988; Parker, 1991), and Peet (1978) and Allen et al., (1991) used a series of these diagrams to quantify changes in the distribution of forest vegetation across Rocky Mountain landscapes. Here, we use gradient diagrams to compare variation in forest distribution with respect to standard elevation and topographic-moisture axes across the five focal landscapes.

To characterize forest compositional change with respect to change in soil nutrient levels, stands within each landscape were separated into three nutrient classes. Our previous research in four of the five landscapes in this study identified pH and extractable manganese (Mn) as the soil factors exhibiting the strongest association with major species composition and diversity gradients (McLeod, 1988; Patterson, 1994; Newell, 1997; Newell and Peet, 1996, 1998). Consequently, we chose Mn and pH as potential measures of soil nutrient status. pH is often used as a measure of fertility and, in general, is a reasonable indicator of soil nutrient availability (Brady, 1974). Stands were divided into three pH classes (low-pH 3.9; mid-pH 4.0-4.9; high-pH 5.0). Manganese is known to precipitate readily in acidic, well-drained soils (Collins and Buol, 1970) and probably serves as a surrogate for the combined influence of original fertility and degree of leaching. Within the pH range of sites in this study, Mn has been shown to be highly positively correlated with pH and site moisture status (McLeod, 1988; Newell and Peet, 1998; Newell, 1997) and to exhibit a particularly strong correlation with vascular plant species richness (e.g., Newell and Peet 1998). The range of log-transformed Mn levels within each of the five landscapes was more consistent than pH and thus came closer to providing a standard measure for comparison of forest distribution across nutrient levels. Sites

were divided into three Mn groups, with boundaries between groups defined as approximately one half standard deviation either side of the mean (log (ppm) mean of -2.724, SD of 1.4). Infertile, low-nutrient sites included stands with log-transformed Mn values -3.4 , mid-nutrient stands = -3.39 to -2.7 and nutrient-rich stands -2.69 . Plots from the Black Mountains and Thompson River lacking soil information were excluded from gradient diagram analyses.

A community classification was generated using Ward's minimum variance cluster method (Ward, 1963). This robust, widely-used agglomerative algorithm (Orloci, 1975; Feoli and Gerdol, 1982; Pielou, 1984; Belbin and McDonald, 1993) identifies clusters using minimized within-cluster variance which is defined as the sum of squares of the distances between every point and the centroid of the cluster (Gauch, 1982; Pielou, 1984). The coefficient of community value (Bray and Curtis, 1957) was used to generate a distance matrix based on species cover. Ward's method was implemented in SAS 6.10 using PROC CLUSTER; SAS Institute Inc., (1995). A TRIM value of 5 was used to remove unusual (outlier) plots from the classification. Plots lacking soil information were included in the classification to ensure that the full range of vegetation composition of each of these five study areas was incorporated into the classification.

Gradient Diagrams

The classification grouped 647 stands into six broad vegetation classes (Figure 2). Groupings were accepted at $R^2 = 0.248$ as this level provided a workable number of classes distributed across the region. Although each vegetation class could readily be subdivided into more homogeneous subclasses, only the broader, regionally-distributed classes were used in the present study so as to facilitate comparisons between localities. Nine of the original 658 plots, representing grasslands and shrub balds from the Black Mountains were trimmed from the classification as outliers by the TRIM function. These plots were excluded from further analyses.

For each of the five landscapes, gradient diagrams were constructed representing each of the three nutrient regimes. This procedure was performed twice using Mn and pH respectively as the basis of the soil nutrient categorization. Stands were plotted on the diagram using consistent elevation and topographic-moisture axes and were identified by their respective vegetation class. Stands lacking soil information and thus not plotted

Landscapes:

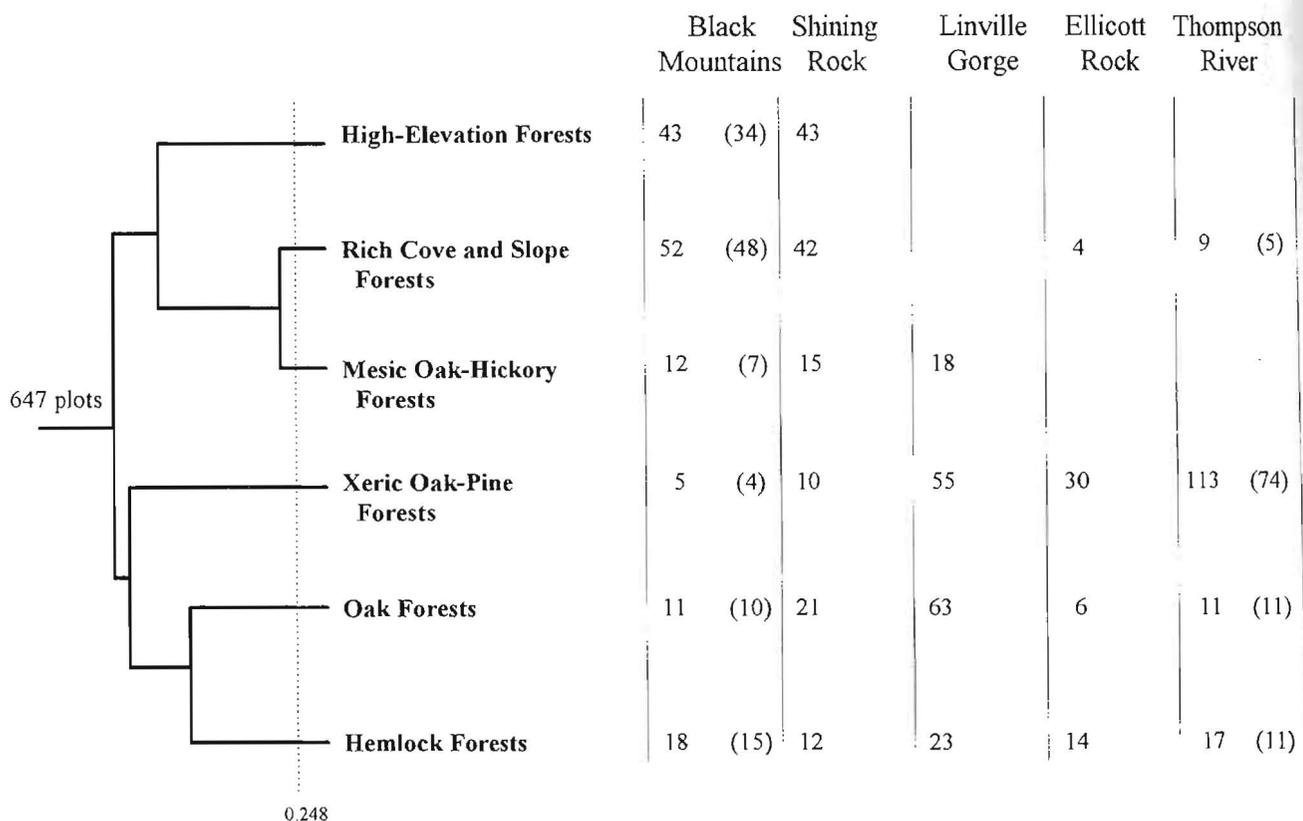


Figure 2.—Classification dendrogram showing the six vegetation classes. Groups were accepted at $R^2 = 0.248$ (level represented by the dashed line). Numbers of stands in each vegetation class are given by locality. Totals represent stands identified in the cluster analysis and gradient diagrams except that, where soils data were not available for all samples, the number of stands in parentheses indicates the number for which soils data were available and which were used in the gradient diagrams.

RESULTS

were well distributed throughout the range of vegetation classes presented. Their absence should not significantly alter vegetation patterns apparent in the gradient diagrams.

For gradient diagrams based on different pH levels, three of the five landscapes were only represented in two of the three nutrient levels. No general patterns could be found because stands within a single vegetation class were also not closely associated with each other, but rather were broadly scattered across the diagram. However, distributional patterns were much clearer in the manganese-based diagrams, with stands generally positioned adjacent to other members of the same vegetation class. For this reason we present only the manganese-based gradient diagrams (Figures 3-7) for comparisons of vegetation class distribution patterns across the five landscapes.

The **High-Elevation Forests** vegetation class is restricted to Shining Rock and the Black Mountains. Stands within this class are dominated by *Betula allegheniensis*, *Fagus grandifolia*, *Picea rubens* or *Quercus rubra*. **High-Elevation Forests** are distributed across all three nutrient levels in both high-elevation landscapes (Figures 3,4). However, high-nutrient stands are nearly absent at the Black Mountains, perhaps reflecting higher leaching of soils on more exposed upper-slopes in this landscape.

The canopy of the **Rich Cove and Slope Forests** is dominated by *Tilia americana* var. *heterophylla* or *Liriodendron tulipifera*, with *Fraxinus americana* and species of *Quercus* and *Carya* also present. This class is characterized by a species-rich herbaceous layer and a near-absence of ericaceous shrubs. **Rich Cove and Slope**

GEOGRAPHIC VARIATION IN FOREST DISTRIBUTION

BLACK & CRAGGY MOUNTAINS

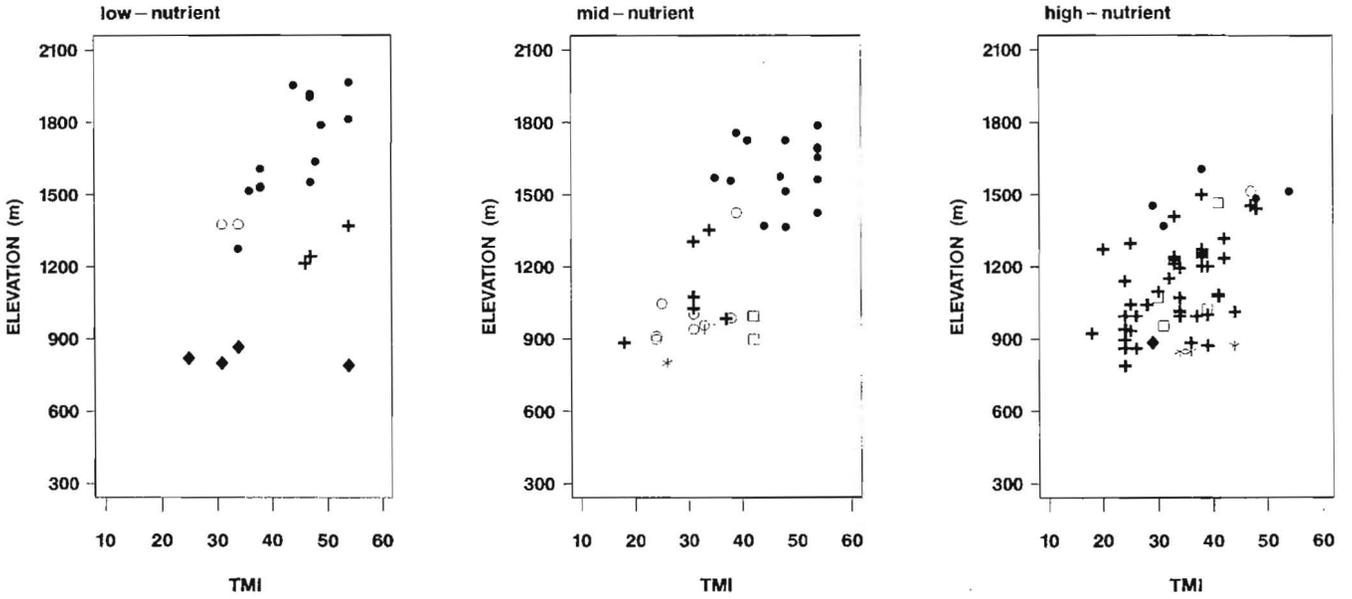


Figure 3.—Gradient diagrams of the Black and Craggy Mountains (Black Mountains) showing the distribution of forest vegetation classes identified using Ward's clustering method (see Figure 2). The three diagrams represent the three standard nutrient levels. Stands are classified by their vegetation class and are plotted by elevation and topographic-moisture (TMI). Increasing TMI values correspond to increasingly xeric conditions. Vegetation classes are represented by the following symbols:

• = High-Elevation Forests, + = Rich Cove and Slope Forests, □ = Mesic Oak-Hickory Forests, ◆ = Xeric Oak-Pine Forests, * = Oak Forests, ○ = Hemlock Forests.

SHINING ROCK WILDERNESS

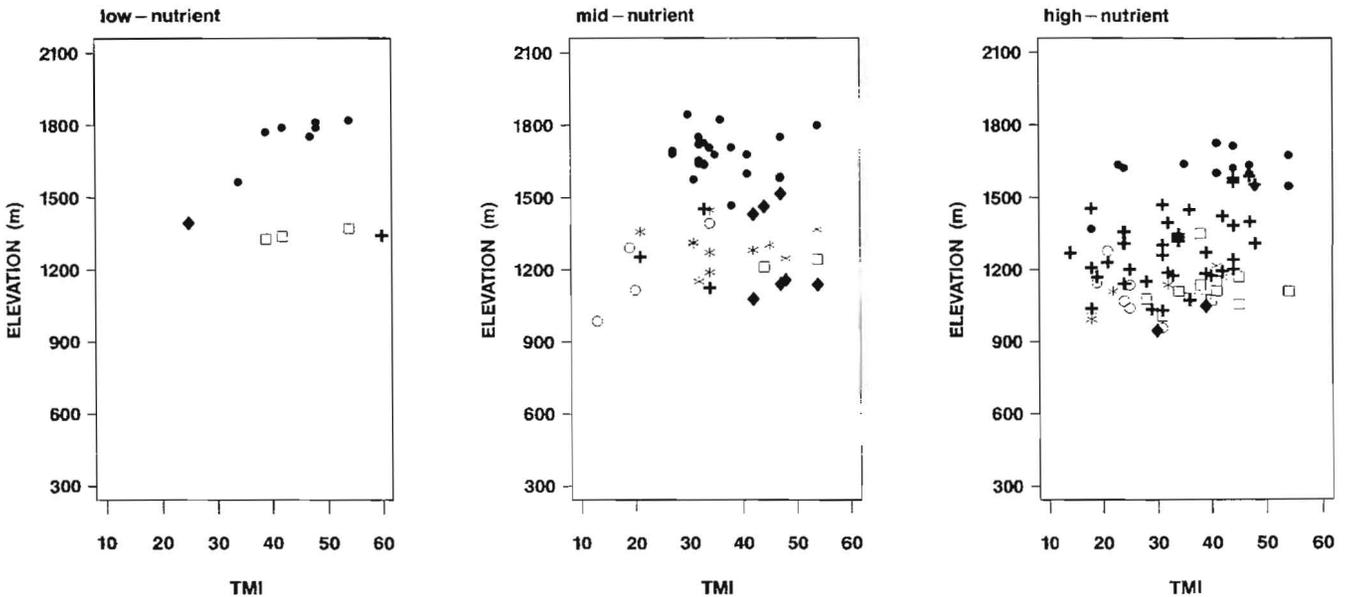


Figure 4.—Gradient diagrams of Shining Rock Wilderness (Shining Rock) showing the distribution of forest vegetation classes. See Figure 3 for details.

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SHINING ROCK WILDERNESS

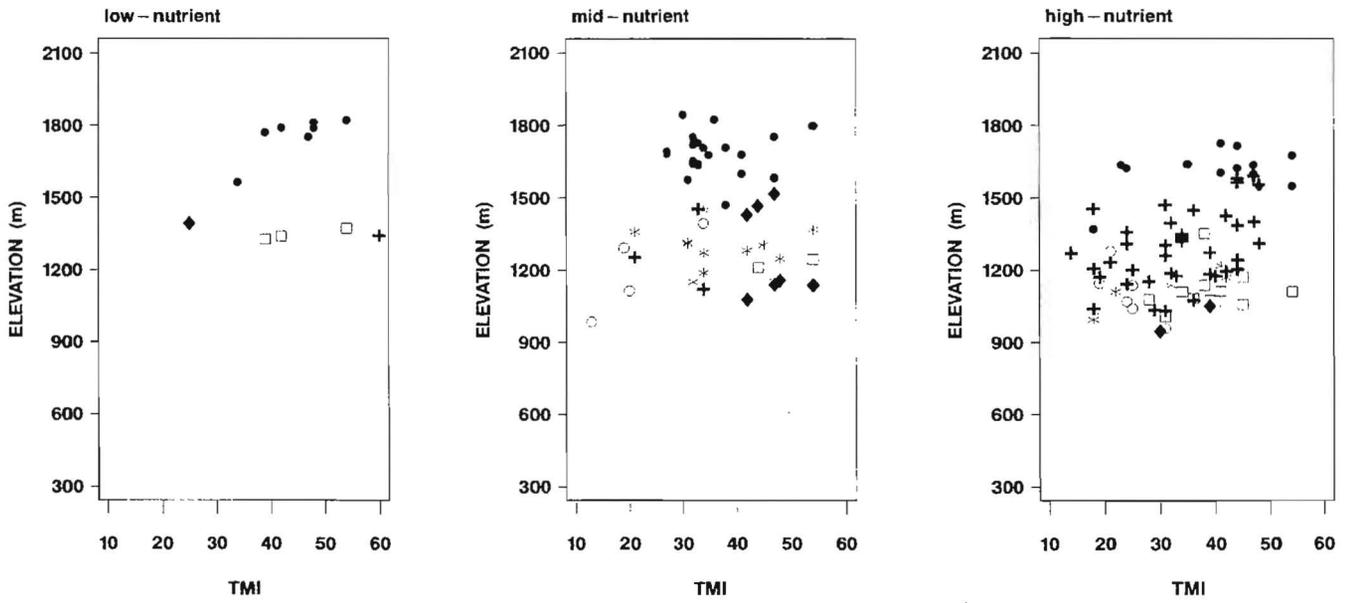


Figure 5.—Gradient diagrams of Linville Gorge Wilderness (Linville Gorge) showing the distribution of forest vegetation classes. See Figure 3 for details.

ELLCOTT ROCK WILDERNESS

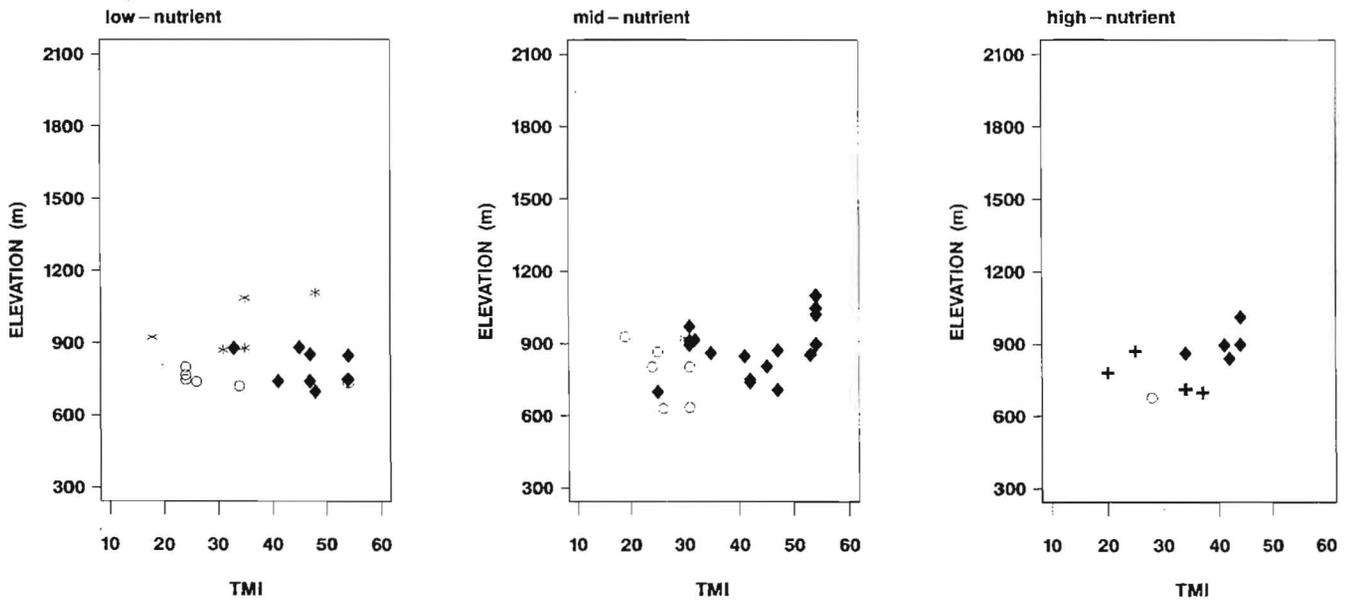


Figure 6.—Gradient diagrams of Ellicott Rock Wilderness (Ellicott Rock) showing the distribution of forest vegetation classes. See Figure 3 for details.

GEOGRAPHIC VARIATION IN FOREST DISTRIBUTION

THOMPSON RIVER GORGE

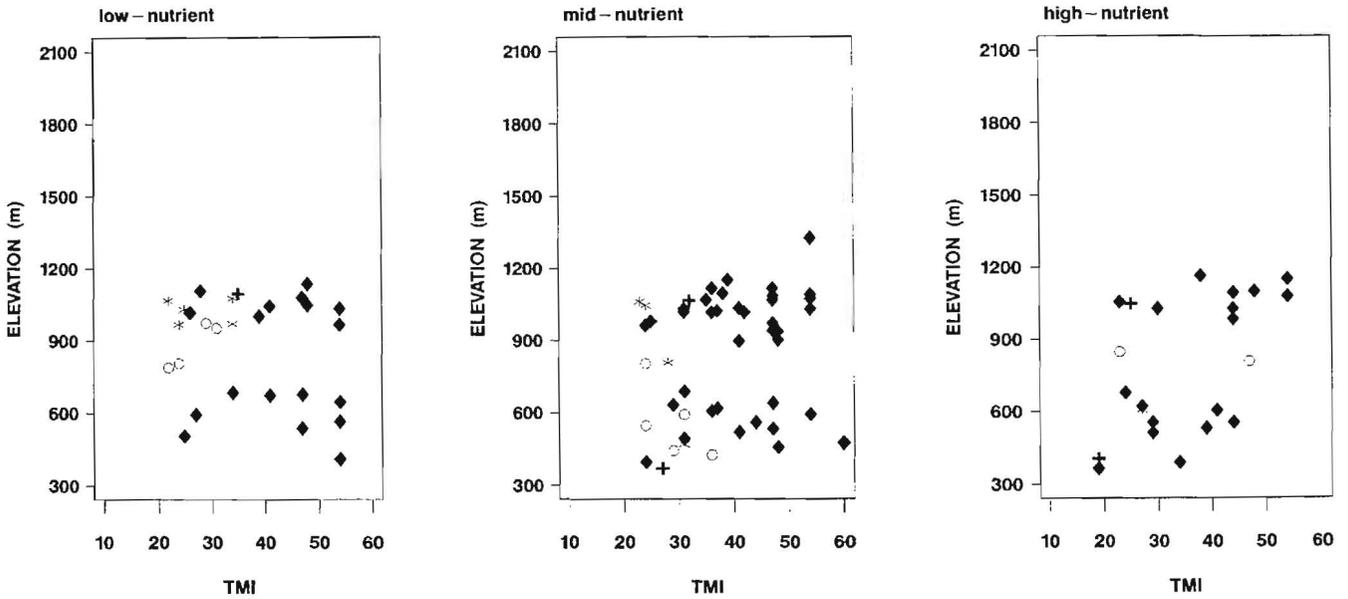


Figure 7.—Gradient diagrams of the Thompson River Gorge (Thompson River) showing the distribution of forest vegetation classes. See Figure 3 for details.

Forests have only limited distribution in the two escarpment landscapes and are absent from Linville Gorge. Where present, this vegetation class is best represented on nutrient-rich sites (Figures 3-7). At Ellicott Rock, **Rich Cove and Slope Forests** are restricted to moist (corresponding to low TMI values), nutrient-rich sites, while at the two high-elevation landscapes this class dominates a wider range of topographic conditions on nutrient-rich sites. Low rainfall levels and highly acidic quartzite bedrock may account for the absence of this class at Linville Gorge, whereas in the two high-elevation landscapes cooler temperatures, high rainfall and typically more base-rich underlying rock may account for the dominance of **Rich Cove and Slope Forests** across a broad topographic range. Warm temperatures in low-elevation escarpment landscapes (Ellicott Rock, Thompson River), may restrict this class to mesic sites.

Mesic Oak-Hickory Forests dominated by species of *Quercus* and usually *Carya*, such as *Q. rubra* and *C. glabra*, typically have a species-rich herbaceous layer and a near-absence of ericaceous shrub species. These forests are typically restricted in elevational and topographic range in comparison to other vegetation classes (Figures 3-7), inhabiting moderate- to high-topographic positions within a consistent narrow (800-1300 m) elevational band at the Black Mountains, Linville Gorge and Shining Rock. However, on nutrient-

rich sites at Linville Gorge this class inhabits a broader elevational range than at the other landscapes, which probably relates to the close association between this class and underlying nutrient-rich meta-arkose and phyllite bedrock (Newell and Peet, 1998). In contrast to Linville Gorge, the two low-elevation, high-rainfall escarpment landscapes lack **Mesic Oak-Hickory Forests**. There is no obvious explanation for the absence of this class in these landscapes, although differences in the natural fire regime driven by rainfall differences may be partially responsible.

Quercus montana and *Q. rubra* are the major canopy species of the **Oak Forests**. Shrub composition varies in this class with *Kalmia latifolia* present on drier, upper-slope sites, and *Rhododendron maximum* a feature of the more sheltered, lower-slope sites. **Oak Forests** are present across all five landscapes, mostly on low- and mid-nutrient sites in the three lower-elevation landscapes and on mid- and high-nutrient sites at the two high-elevation localities (Figures 3-7). This class has limited distribution in the Black Mountains, perhaps relating to more base-rich bedrock. **Oak Forests** inhabit a broad range of topographic conditions, but are typically concentrated on mid-topographic positions on low- and mid-nutrient sites. However, at Thompson River this class is restricted to mesic conditions which perhaps relates to the lack of recent, low-intensity fire in this landscape

and the dominance of **Xeric Oak-Pine Forests** across most topographic conditions. **Oak Forests** span the elevation range at Linville Gorge, probably reflecting the lower rainfall of this landscape and the generally acidic underlying bedrock.

Xeric Oak-Pine Forests are dominated by relatively drought-tolerant canopy species such as *Quercus montana*, *Q. coccinea*, *Pinus pungens*, *P. rigida* and *P. virginiana*, with *P. echinata* and *P. strobus* also present at Ellicott Rock and Thompson River. This class has a distinctive ericaceous shrub layer, typically dominated by *Kalmia latifolia*, but with *Gaylussacia ursina* also prominent at Ellicott Rock and Thompson River. **Xeric Oak-Pine Forests** inhabit exposed or thin-soiled topographic positions on all five landscapes (Figures 3-7). This class has limited distribution at the two high-elevation landscapes but its best development on these landscapes is on low-nutrient sites at the Black Mountains and mid-nutrient sites at Shining Rock. In the three lower-elevation landscapes this vegetation class is present on thin soils across all nutrient levels. At Linville Gorge this class is dominant on xeric, nutrient-poor sites, which contrasts with Ellicott Rock and Thompson River where **Xeric Oak-Pine Forests** are dominant across a wide range of topographic positions for all three nutrient regimes. Differences in the distribution of this class between the three low-elevation landscapes might be expected to relate to rainfall and underlying rock type. However, the low-rainfall Linville Gorge landscape, underlain predominantly by highly acidic rock, has restricted **Xeric Oak-Pine Forests** distribution, whereas this class dominates the two high-rainfall escarpment landscapes. Such inconsistencies in distribution may partly relate to differences in topographic shape between the Linville Gorge and escarpment landscapes. The highly dissected topography of Linville Gorge produces sharp, distinct vegetation changes across the topographic-moisture gradient, whereas vegetation change may be more gradual across the gentler sloping topography of Thompson River and Ellicott Rock. Widespread **Xeric Oak-Pine Forest** dominance in the escarpment landscapes may be an artifact of past widespread disturbance by logging and subsequent catastrophic fire. It is also likely that the coarse scale of our classification obscures subtle patterns within this vegetation class.

Tsuga canadensis is the major canopy species of the **Hemlock Forests**, with *Betula lenta*, *Liriodendron tulipifera* and *Pinus strobus* present at some sites. Stands typically have a dense *Rhododendron maximum* shrub layer and low

overall species richness (Wentworth, 1980; McLeod, 1988; Patterson, 1994; Newell, 1997; Newell and Peet, 1996, 1998). The restriction of **Hemlock Forests** to relatively infertile, mesic sites in all five landscapes is consistent with previous studies (Figures 3-7; Whittaker, 1956; McLeod, 1988; Schafale and Weakley 1990). This vegetation class is distributed across both low- and mid-nutrient sites in four of the localities. In contrast, at Shining Rock **Hemlock Forests** occur on sites with mid- and high-nutrient status. There is no obvious reason for this atypical distribution at Shining Rock, except that intense logging in the past and subsequent catastrophic burning may have relaxed competition and blurred species distribution patterns. For example, *Rhododendron maximum* successfully colonizes more quickly and once established is likely to inhibit other species from invading. Alternatively, absence of **Hemlock Forests** from low-nutrient sites at Shining Rock may reflect the lack of infertile lower-slope and cove sites in this landscape.

DISCUSSION

Comparisons with the Great Smoky Mountains gradient model

Whittaker (1956) showed that vegetation of the Great Smoky Mountains was distributed primarily along topographic-moisture and elevation gradients, a result reaffirmed in numerous subsequent landscape-scale studies elsewhere in the Southern Appalachian Mountains. However, these previous studies have not examined the consistency of compositional gradients across multiple Southern Appalachian landscapes. In this study we have examined how specific forest communities change in distribution with respect to elevation and topographic position across three nutrient regimes and five landscapes. Patterns in the two high-elevation landscapes (Black Mountains, Shining Rock) follow Whittaker's model, with the addition that vegetation also varies with soil nutrients. However, in the three low-elevation landscapes (Ellicott Rock, Linville Gorge, Thompson River) vegetation composition is strongly correlated with nutrient and topographic-moisture gradients, but has a weaker association with elevation. Differences between the three low-elevation gradient models and two high-elevation models are consistent with a hypothesis by Newell (1997) that the more highly dissected topography of mid- and low-elevation landscapes contains a broader range of topographic and soil conditions (e.g. a gradient from highly exposed, xeric, infertile ridges to sheltered, nutrient-rich coves) than high-elevation

landscapes which tend to have less dissected topography and generally more exposed sites with thin soils of limited development. Newell (1997) also suggest that in high-elevation landscapes the extreme conditions associated with elevation allow it to override other environmental factors and have a primary influence on vegetation distribution. In contrast, in mid- and low-elevation landscapes more dramatic landform differences heighten topographic and soil extremes, seemingly overriding the overlying elevation gradient (Newell, 1997).

Most studies of Southern Appalachian forests have used Whittaker's (1956) two-dimensional model of vegetation as the standard for examining vegetation distribution patterns. Although our analysis uses coarser-scale vegetation groups than the landscape-scale Whittaker (1956) study, comparisons are revealing. Our results have shown that the distributions of some specific vegetation classes, such as **Hemlock Forests**, closely correspond with environmental conditions described in previous landscape-scale studies. However, while Whittaker (1956) and subsequent researchers (e.g., Golden, 1981; Callaway et al., 1987; Schafale and Weakley, 1990) suggest that **Rich Cove and Slope Forests** are typically restricted to mesic, nutrient-rich lower-slopes and coves, our research has shown that this is true only in one of the five landscapes studied (Ellicott Rock). Whittaker (1956) and McLeod (1988) both show a broadening in the distribution of this vegetation class with increasing elevation, but still suggest a more restricted distribution than has been observed in this study. The predominance of **Rich Cove and Slope Forests** on nutrient-rich sites is also more clearly demonstrated in this present study than in previous studies where vegetation composition was described under one general set of nutrient conditions. Moreover, our qualitative observations on especially fertile sites developed over amphibolites elsewhere in the Southern Appalachians suggest that forests closely allied with **Rich Cove and Slope Forests** can occupy essentially all topographic positions. Similarly, **Xeric Oak-Pine Forests** have traditionally been associated with infertile, xeric ridgelines and south-facing slopes in the Southern Appalachians (Whittaker, 1956; Cooper and Hardin, 1970; Schafale and Weakley, 1990), but our results from the infertile southern escarpment region suggest that they can inhabit a broad range of topographic conditions.

Although there are general similarities in the distribution of vegetation across the five landscapes, the breadth and position of specific vegetation classes vary with respect to elevation,

topographic-moisture and soil nutrient gradients. Landscape-level shifts in vegetation class position are most likely a response to underlying geology, differences in rainfall patterns, and other climatic differences rather than changes associated simply with latitude. In the two high-elevation landscapes, vegetation classes inhabiting high-elevation positions have relatively consistent distributions, with subtle differences between the classes present at lower-elevations within these landscapes. In both landscapes **High-Elevation Forests** inhabit a broad range of topographic positions on all three nutrient regimes. The mid-elevation dominance of **Rich Cove and Slope Forests** on nutrient-rich sites is also similar in the two landscapes. However, at Shining Rock the restriction of this class to nutrient-rich sites contrasts to its distribution across all three nutrient regimes at the Black Mountains. Similarly, while the **Xeric Oak-Pine Forests**, **Mesic Oak-Hickory Forests** and **Oak Forests** inhabit similar topographic positions at both high-elevation landscapes, they shift in position along both the elevation and nutrient gradients, inhabiting higher elevation sites with higher nutrient status at Shining Rock. Such differences in vegetation class distribution probably result from the more acidic bedrock types at Shining Rock.

The differences in the distribution of vegetation classes across the three low-elevation landscapes are less subtle, with patterns at Linville Gorge deviating from those observed at the two more southern escarpment landscapes. At Linville Gorge, nutrient-rich sites are dominated by **Mesic Oak-Hickory Forests**, whereas this class is absent from the two escarpment landscapes with **Xeric Oak-Pine Forests** typically dominant on nutrient-rich sites. On the two escarpment landscapes drought-tolerant **Xeric Oak-Pine Forests** dominate a wider range of topographic and nutrient conditions than at Linville Gorge where they are restricted to xeric, mid- and low-nutrient sites. There is also a shift in position of **Oak Forests**. In the escarpment landscapes this class is restricted to mesic sites, in contrast to Linville Gorge where it inhabits mid-topographic positions. Past land-use differences (discussed below) may account for some of these landscape-level differences in vegetation class distribution.

There are marked differences in the distribution of those vegetation classes present in all five landscapes, with shifts in position along nutrient, topographic and elevation gradients from one landscape to another. For example, **Oak Forests**, typically restricted to low- and mid-nutrient sites at the three lower-elevation landscapes, move to more

fertile, mid- and high-nutrient sites at the two high-elevation landscapes. We suggest that as a vegetation class moves to high-elevations it will inhabit more fertile site conditions which perhaps compensates for environmental stresses associated with a rise in elevation; for example, less favorable temperatures, a shorter growing season and typically more exposed site conditions. This may explain the occurrence of **Hemlock Forests** on nutrient-rich, high-elevation sites at Shining Rock, whereas elsewhere this class is typically associated with highly infertile sites. Similarly, the presence of **Mesic Oak-Hickory Forests** on more fertile, higher-elevation sites at Shining Rock than in the Black Mountains is consistent with this hypothesis. However, for some vegetation classes distributed across all five landscapes (e.g., **Xeric Oak-Pine Forests**) other factors, such as differences in land-use history, are likely to be at least partially responsible for differences in distribution between landscapes.

Deviations from the Great Smoky Mountains model: factors that vary with geography

The breadth and position of specific vegetation classes vary with respect to elevation, topographic-moisture and soil nutrient gradients across the five Southern Appalachian landscapes used in this study. Such inconsistencies in vegetation distribution most likely relate to the spatial variation in environmental factors and past disturbance events. Factors associated with two major spatial scales appear to account for many of the inconsistencies in vegetation distribution.

Large, subregional-scale variation in environmental conditions influence the consistency of vegetation distribution. Subregional differences in rainfall are influenced by subregional differences in topography. For example, the sharp topographic barrier of the southern escarpment forces moisture-laden air from the south over the mountains in this subregion, resulting in local high annual rainfall levels. By contrast, the broad, low-elevation Asheville basin experiences primarily descending air and low annual rainfall levels (Kopec and Clay, 1975). Latitudinal differences probably account for the warmer temperatures of the two southern escarpment landscapes as compared to Linville Gorge, whereas smaller-scale altitudinal differences are responsible for cooler temperatures at Shining Rock and the Black Mountains than the three low-elevation landscapes. Historic events, such as post-Pleistocene warming have isolated individual species and groups of species within specific subsections of the Southern Appalachian Mountains (e.g., see Ramseur, 1960; Wiser,

1994). For example, *Gaylussacia ursina*, dominant in **Xeric Oak-Pine Forests** at Thompson River and Ellicott Rock, is restricted to 12 counties south of the Asheville Basin (Weakley, 1996). Geographic proximity may allow an influx of species that would usually not occur in Southern Appalachian vegetation classes; for example *Pinus echinata*, typically a piedmont species, is present in both escarpment landscapes. Subregional differences in underlying bedrock types also increase geographic variation in the distribution of vegetation classes across the Southern Appalachian region.

At a finer scale, landscape-level differences in environmental factors and past disturbance history also influence the consistency of vegetation distribution between landscapes. The predominance of the normally drought associated **Xeric Oak-Pine Forests** in the two high-rainfall escarpment landscapes and their more limited distribution at low-rainfall Linville Gorge suggests that factors other than rainfall influence the distribution of this vegetation class. Landscape-level differences in topographic shape and disturbance history may play a large role. Topographic shape influences factors such as site exposure, soil moisture and nutrient leaching and accumulation (Selby, 1985). The topography of Linville Gorge is much more dissected than those of Ellicott Rock and Thompson River, suggesting the existence of greater extremes in site and soil conditions in this landscape. Topographic differences, and associated differences in the range of site conditions present, may explain differences in the breadth and position of vegetation classes on both the topographic-moisture and nutrient gradients in these three landscapes. At Linville Gorge vegetation classes have distinct, fine-scale separation along these two gradients, contrasting to the less distinct and broader distribution of classes in the less-dissected escarpment landscapes. Alternatively, differences in vegetation breadth and position may reflect variation in past disturbance regimes. The absence of broad-scale logging and subsequent catastrophic fires in Linville Gorge might account for the apparently sharper differentiation of vegetation across environmental gradients in this landscape, whereas the impact of these past disturbances in the two escarpment landscapes may be responsible for indistinct class separation. These high-impact disturbances may have relaxed competition between species and blurred species distribution patterns in Ellicott Rock and the Thompson River, whereas discrete vegetation class patterns at Linville Gorge suggest that, in the absence of

catastrophic disturbance, species are strongly associated with specific environmental conditions.

Differences in the natural, presettlement fire regime between the three low-elevation landscapes may account for the dominance of different vegetation classes at Linville Gorge and the two escarpment landscapes. At Linville the restriction of *Pinus*-dominated communities to dry ridges, coupled with fire-scar evidence and the abundance of *Quercus*-dominated vegetation classes, indicates a past high-frequency, low-intensity fire regime (7-12 year frequency; Frost, 1995; Newell and Peet, 1998). In contrast, the high-rainfall escarpment landscapes probably had infrequent fires (>12 year frequency; Frost, 1995), which could account for the limited presence of *Quercus*- and *Carya*-dominated communities in these two regions. However, the near absence of *Quercus* and *Carya* regeneration in present-day Linville Gorge vegetation classes, associated with the loss of the natural fire regime, suggests that the *Quercus* dominance of this landscape will decline (Newell, 1997).

Factors responsible for the differences between Linville Gorge and sites of similar elevation in the two high-elevation landscapes are less obvious than those associated with the three low-elevation landscapes and probably relate mostly to rainfall and underlying bedrock. The greater dominance of **Xeric Oak-Pine Forests** and absence of **Rich Cove and Slope Forests** at Linville Gorge is likely to result from lower rainfall and more acidic, infertile soils as compared to the landscapes of the Black Mountains and Shining Rock.

Factors that potentially explain differences in the distribution of vegetation between the two high-elevation landscapes are more subtle than those influencing the three low-elevation landscapes. This probably reflects the similarity of environmental conditions in these two landscapes, particularly in temperature, range and length of growing season and rainfall levels. Past logging and fire may also have blurred differences in the distribution of vegetation classes between these landscapes.

CONCLUSIONS

Although Whittaker's (1956) model continues to provide a conceptual starting point for regional vegetation comparisons, the increasing availability of techniques for quantifying complex environmental gradients, coupled with detailed knowledge of vegetation across a much greater number of landscapes in the Southern Appalachian region and recognition of the importance of soil nutrient levels, provides an

opportunity to study vegetation biogeographic patterns in much greater detail than has previously been possible. The present study represents a first attempt at such biogeographic synthesis. Using a standard environmental framework we were able to show that while vegetation patterns change across elevation, topographic-moisture and soil nutrient gradients, a complex interplay of factors such as climate, geology and land-use history influences these patterns.

Vegetation studies in the Southern Appalachian Mountains should focus on the role of soil nutrients. Moreover, landscape-scale variation in vegetation distribution makes clear the importance of placing local, landscape-level knowledge in a regional context to understand geographic changes. Additional research using a large number of datasets distributed across the broad range of climatic conditions of the Southern Appalachian Mountains will be needed to tease apart and understand the complex biogeographic patterns of this region.

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