INFLUENCES OF THE EVERGREEN UNDERSTORY LAYER ON FOREST VEGETATION COMMUNITIES OF THE CENTRAL APPALACHIAN HIGHLANDS

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ABSTRACT.—Evergreen understory communities dominated by *Rhododendron maximum* and/or *Kalmia latifolia* may exert significant controls on regeneration of overstory trees and nutrient retention in central Appalachian forests, but the regional distribution and ecological importance of these communities are poorly documented. We employed leaf-off satellite remote sensing combined with field sampling and quantitative analyses to assess patterns of *R. maximum* and *K. latifolia* distribution. We compared topographically mediated distributions of these species in the warm and dry Ridge and Valley physiographic province and on the cooler and wetter Allegheny Plateau. The spatial extent of each understory community (either *R. maximum* or *K. latifolia)* was estimated with greater than 80 percent accuracy using leaf-off Landsat data combined with topographic data. Using clustering analysis and non-metric multidimensional scaling (NMS) with plot survey data, we found that *R. maximum* and *K. latifolia* varied from each other in their species associations, and that topographic exposure, relative wetness, and intensity of gypsy moth defoliation were the chief environmental variables explaining differences in distribution between the two study areas. ANOVA demonstrated significant differences in mid-story volume of canopy tree species where evergreen understory species were prominent, indicating that these communities substantially influence overall forest structure, stand dynamics, and regeneration.

Introduction

In the eastern United States, the Appalachian highlands region contains perhaps the most extensive contiguous area of forests, since the high amount of topographic relief has precluded their large-scale transformation into agricultural or urban land uses (Robison 1960). These forest ecosystems provide a number of societal services on the regional scale (Daily et al. 1997), including the maintenance of air and water quality, sediment trapping, flood attenuation, and nutrient storage (Perry 1998, Aber et al. 2000). Moreover, on the global scale these forests also act as a carbon sink capable of attenuating climatic changes caused by increases in atmospheric carbon (Schlesinger 1977, Sedjo 1992, Currie *et al*. 2003). Finally, forest ecosystems are valuable for providing habitat and refuge for wildlife, and are valued for their recreational and aesthetic characteristics. The future sustainability of these societal services depends on the welfare and successful management of forest ecosystems, which in turn entails a thorough understanding of the distribution of individual species and associations of species in these forest communities.

The broad-scale relevance of the evergreen understory species rosebay rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) to Appalachian forests at landscape and larger scales has not been addressed extensively in the literature, despite their wide geographic extent and prominent role in forest ecology where present. *R. maximum* (RMAX) and *K. latifolia* (KLAT) occurring in forest understories in nearly pure stands or mixed in varying proportions have been mapped on the landscape scale in the southern Appalachians, but in the central Appalachian Mountains only plot level analyses of their reproductive behavior and ecological relationships have been performed (Plocher and Carvel 1987, Cooper and McGraw 1988). Their locations are correlated with topography, with RMAX thriving in protected, mesic locations and KLAT more often located on exposed, upslope sites. The different landscape positions inhabited by these two species are characterized by differences in solar radiation, cold air drainage, soil moisture, summer and winter

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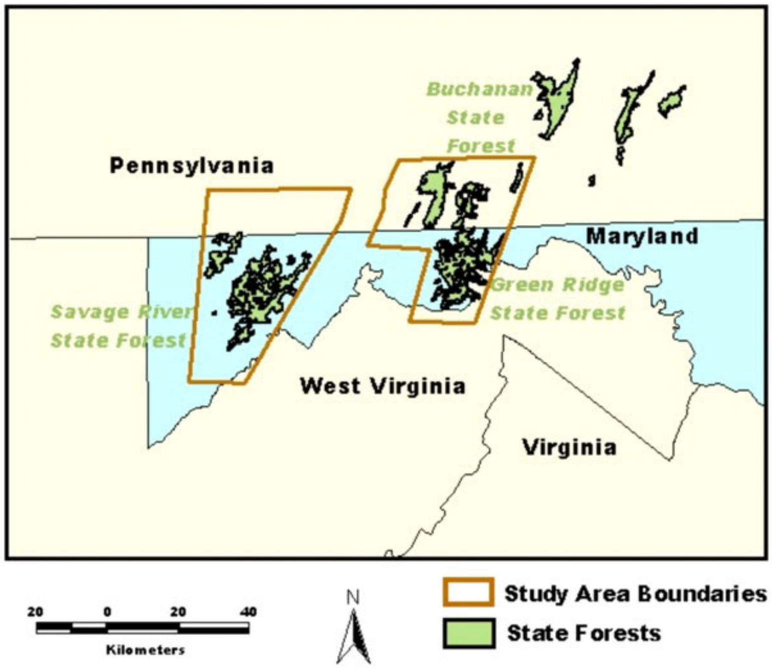

Figure 1.—Area map of present study showing extent of state forest lands.

temperature regimes, and atmospheric drying potentials (Davidson 1966, Monk et al. 1985, Lipscomb and Nilsen 1990a, 1990b, Muller 1991, Dobbs 1995). Existing works suggests that RMAX and KLAT are important component species of Appalachian forests because they:

1) Have the potential for slowing mineral cycling (McGinty 1972, Thomas and Grigal 1976, Monk et al. 1985), and therefore have water quality maintenance implications in the event of disturbance. RMAX has been referred to as a keystone species in this regard (Yeakley et al. 1994);
2) Inhibit canopy tree regeneration when present in dense stands (Minkler 1941, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Baker and Van Lear 1998, Nilsen *et al.* 1999, Walker *et al*. 1999, Beckage *et al.* 2000, Nilsen *et al.* 2001, Lei *et al*. 2002);
3) Provide forage and refuge for wildlife (Romancier 1970, Gates and Harman 1980, Thackston *et al*. 1982, Johnson *et al*. 1995, Spear 1998, USDA 2002);
4) Are significant components of Appalachian forests with regard to carbon sequestration and nutrient budgets (McGinty 1972, Thomas and Grigal 1976, Monk *et al*. 1985);
5) Enhance the beauty and hence inspirational value of Appalachian forests (Hollenhorst *et al*. 1993);
6) Comprise part of the cultural and ethno-botanical heritage of the Appalachian region, traditionally indicated for a number of medical uses (Sargent 1893, Uphof 1968) and used for craft items (e.g. one common name attributed to KLAT is 'spoonwood') (USDA 2002).

Study Areas

The spatial extent and potential ecological influence of the evergreen understory species RMAX and KLAT were assessed in two representative study areas of the central Appalachian highlands (Figure 1). One study area, encompassing the Green Ridge and Buchanan State Forests in Maryland and Pennsylvania, is located in the warmer and drier Ridge and Valley physiographic province, while the other is located on the cooler and wetter Allegheny Plateau (Savage River, Potomac, and Forbes State Forests in MD and PA). A considerable extent of these study areas is designated as public forest or game lands, and consequently experience less intensive development and logging pressure than adjacent private lands. Because of differences in topography and climate, as well as land use history, the forest community composition and structure of the forest communities in these two study areas are dissimilar from each other, but are representative of a broad range of environmental conditions typically found in the central Appalachian region.

Ridge and Valley Study Area

The Green Ridge State Forest (GRSF) area in Maryland was heavily cut for timber, tanbark, and hoop poles between 1879 and 1910, and wildfires were common in the regenerating forest for a number of years thereafter (Mash 1996). In the early and middle 20th century, much of the area that is now the GRSF was planted in fruit (primarily apple) orchards (Mash 1996). This intense land use history within the GRSF has influenced current forest composition, which is largely devoid of KLAT and RMAX. The current forest of the ridge and valley study area is composed primarily of deciduous trees, mixed with a lesser amount of coniferous trees in the canopy. Our data show that chestnut oak (*Quercus prinus*) comprises 24 percent of the total basal area, followed by red oak (*Quercus rubra*) at 16 percent, white oak (*Quercus alba*) at 13.5 percent, scarlet oak (*Quercus coccinea*) at 7.5 percent, and black oak (*Quercus velutina*) at 6.5 percent (Chastain, unpublished data). Various pines (*Pinus virginiana, strobus, rigida,* and *pungens*) make up 9 percent of the overall basal area in this study area. These forests are largely 50 to 75 years in age (Maryland Continuous Forest Inventory, unpublished data).

Yearly average minimum and maximum temperatures for this study area are 2.3 and 15.8°C, with temperatures rarely exceeding 32°C in the summer months, but regularly dipping below -10°C in the winter (Stone and Matthews 1974). Elevation ranges from 123 to 845 meters, with steep northeast-southwest trending ridges in the GRSF and a larger contiguous upland area in the Martin Hill section of the BSF. The annual precipitation range was 896 – 1297 mm (averaging 1023 mm) for the period 1983-1998 (Lynch, pers. comm.).

Allegheny Plateau Study Area

The Allegheny Plateau study area is considered part of the mixed mesophytic forest by Braun (1950). As with the ridge and valley, this area was largely cut in the 20th century, but has regenerated naturally in the interim. The forest canopy in this study area is primarily deciduous with localized areas dominated by eastern hemlock (*Tsuga canadensis*). Red oak (*Quercus rubra*) comprises 25 percent of the total basal area, followed by red maple (*Acer rubrum*) at 18 percent and chestnut oak (*Quercus prinus*) at 17 percent (Chastain, unpublished data). Hemlock accounts for 5.5 percent of the total basal area. American chestnut was an important component of these forests previous to its extirpation in the early to mid 20th century due to the blight caused by the fungus *Cryphonectria parasitica* (Braun 1950). The elevation range for the Allegheny Plateau is 304-986 meters, with a humid continental climate characterized by severe winters and mild summers. The annual precipitation range between 1983 and 1998 was 913 – 1490 mm, with an average of 1216 mm (Lynch, pers. comm.).

Methods

The spatial extent and distribution of RMAX- and/or KLAT-dominated evergreen understory communities in each study area was first mapped using satellite imagery combined topographic information (Chastain and Townsend in review). A forest community classification was developed from the floristic (plot) data and ordination was used to assess patterns of species composition and examine relationships with hypothesized environmental gradients. Finally, an analysis of variance (ANOVA) was performed to examine differences in forest vertical structure between stands with an evergreen understory layer and those without. Hypotheses tested during these analyses include:

1) Multispectral remote sensing image data combined with topographic information can be successfully applied to accurately map the RMAX and KLAT-dominated evergreen understory communities on the landscape and regional scales.

2) Forest composition and structure are related to the presence of the evergreen understory layer, and these characteristics are different from forests that do not contain an evergreen understory. That is, canopy tree regeneration is inhibited by dense evergreen understories, and is manifested in a simplified structure where KLAT and RMAX are present.

3) Due to differences in topographic patterns, moisture and disturbance regimes, and land use histories between the two study areas, different environmental factors control the pattern of forest communities in general and evergreen understory communities specifically. Therefore, KLAT and RMAX-dominated communities should be distinct compared to other community types, and vary from each other in their distribution in ordination space between the two study areas.

Vegetation Sampling Design

The vegetation composition and structure data were obtained through the establishment of 213 vegetation survey plots between 1999 and 2002. The plot layout followed Townsend and Walsh (2001), with two crossing 60 meter transect tapes and five sample points located at the end of the transects and at their intersection. The orientation of the first transect line was pre-determined randomly. This plot design was chosen because it has the dual utility of efficiently supporting vegetation community analysis and also has been determined to be favorable for remote sensing vegetation studies (Grosenbaugh 1952, Lindsey et al. 1958, Justice and Townshend 1981). Basal area (BA) was estimated at each of the sample points using a metric factor-2 Bitterlich prism. Tree height measures (top and bottom of leaf canopy) were taken for three canopy and subcanopy trees at each sample point using a laser rangefinder. Heights (top and bottom of leaf canopy) were noted for all shrub/sapling strata species present with greater than 15 percent coverage. Cover estimates were made for the canopy, subcanopy, shrub/sapling, and herb layers as a whole and by species. Finally, leaf area index (LAI) was estimated at these plots using hemispherical photography acquired just above the height of the evergreen understory vegetation where present and at a height of 1 meter where no evergreen understory was present. Out of the 213 vegetation plots visited, 105 are located on the Allegheny Plateau and 108 in the Ridge and Valley province. Observations obtained within these plots were found to be comparable to data acquired in over 800 Maryland continuous forest inventory (CFI) plots established in these two study areas, so the field data from which this study is based are considered representative of regional forest characteristics.

Because of the linear nature of some evergreen understory patches (i.e. along streams or ridges) and logistical concerns, plots representing the evergreen understory were limited to one 60 meter transect with three sample points - one at each end and one in the middle. So that all data points were consistent and all analyses were comparable, plots having two perpendicular transects were analyzed using only one randomly-selected transect.

Evergreen Understory Community Mapping

The maps used to represent the spatial extent and distribution of evergreen understory communities in the two study areas were developed from supervised and decision tree classifications of leaf-off (March 31, 2000) Landsat Enhanced Thematic Mapper (ETM) imagery and topographic data derived from a digital elevation model (DEM). Field samples were used as training data for the remote sensing maps. This work indicated that topographic data improved the mapping of evergreen understory communities over Landsat data alone by spatially differentiating RMAX and KLAT by their disparate ecological niches, and is described in detail by Chastain and Townsend (in press).

Forest Community Classification

A cluster analysis using Ward's minimum variance method (Lance and Williams 1967) was performed to distinguish discrete forest vegetation classes (communities) in the vegetation survey data. Dissimilarity among plots was computed using the Sorenson statistic (Bray and Curtis 1957) based on an importance value (IV), which was calculated as a sum of the relative basal area (RBA) and percent coverage of the individual species. The IV was used to positively weight the evergreen understory shrub species whose basal area was often low when computed using the Bitterlich variable plot method. Ward's method was then implemented in the SAS statistical software, producing an agglomerative hierarchical classification that could be used to distinguish groups of plots dominated by KLAT, RMAX, or neither in the subsequent analyses.

Table 1.—Descriptions, computations, and references for the various topographic indices used in the classifications performed for the Ridge and Valley and Allegheny Plateau study areas.

Name	Acronym	Computation	Reference
Transformation	BEERS	cos(aspect – 45) + 1	Beers *et al.* 1966
Relative Slope Position	RSP	dist to bottom/(dist to top + dist to bottom) * 100	
Topographic Convergence Index	TCI	$\ln(\alpha/\tan\beta)$	Beven and Kirkby 1979
Terrain Shape Index	TSI	Z'/R where Z' = mean elevation of plot and R = plot radius	McNab 1989
Land Form Index	LFI	sum of slope observations / (N*100)	McNab 1993
Terrain Relative Moisture Index	TRMI	slope position + curvature + slope angle + slope aspect	Parker 1982

Ordination

Nonmetric multidimensional scaling (NMS) ordination was performed using the software PC-Ord (McCune and Mefford 1999) on the species IV scores obtained for the 213 plots. The analyses were conducted using data from both study areas together and separately to determine the extent to which composition varied according to different gradients within each area. Ordination arranges species and samples along one or more dimensions so that similar species and samples are closer together and dissimilar ones are farther apart (Jongman et al. 1995). Ordination is often used in ecology to describe the strongest patterns or gradients of species composition. Statistically, ordination behaves as a data reduction technique that collapses large amounts of information containing many variables (i.e., all the species present in a data set) into a smaller number of composite (synthetic) variables that comprise the majority of the variation in the data set. Ordination assumes that regular patterns of species co-occurrence exist, but, unlike discrete classification techniques, the data are retained in a continuous form.

Species are hypothesized to respond to a number of topographic, disturbance, or resource gradients which can be considered to control the gradients of composition described by the ordination. Correlation and regression are therefore used to relate ordination scores to environmental variables (species abundance is not used because of the large number of zero IV values found in a vegetation data set). Table 1 describes the topographic variables we analyzed with respect to the NMS ordination. In addition, the average annual precipitation (cm) between 1983 and 1998 (Lynch, pers. comm.) on the vegetation plots, percent rock cover, and the number of gypsy moth defoliations were also examined. All of the environmental variables examined were derived from GIS data layers except rock cover, which was observed during field visits.

Forest Structure (ANOVA)

In the southern Appalachians, it has been observed that areas containing dense evergreen understories are structurally simpler than surrounding forests (essentially two-tiered forests consisting of the tree canopy and shrub layer) due to the inhibition of tree regeneration (Hedman and Van Lear 1995, Baker and Van Lear 1998). In addition, KLAT understory communities in Massachusetts were found to favor poorer sites characterized by lower BA and leaf area (Wilson and O'Keefe 1983). In this research, ANOVA was used to test the hypothesis that differences existed between the volume of the mid-story forest strata in areas with an evergreen understory present in contrast to areas where it is absent ('control' plots). The volume of the mid-story was calculated geometrically by averaging the depth of the vegetative matter in three mid-story individuals on each of the three sample points per plot and determining its coverage from the percent coverage data estimated at each plot. This method was followed for each stratum to construct a simple model of forest structure for each plot (Figure 2) in which the canopy, subcanopy, and shrub/sapling layer are represented by volumetric shapes. Similarly,

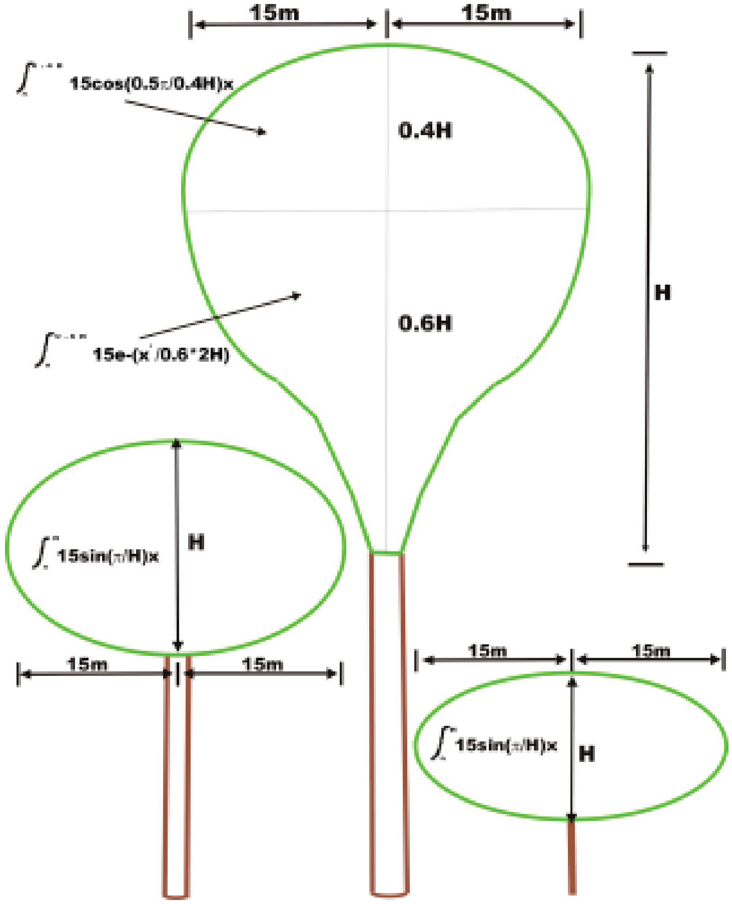

Figure 2.—Schematic drawing of the simplified three-strata model of forest structure as developed for this research.

ANOVA was used to test whether the presence of KLAT or RMAX was associated with lower BA and LAI in these two central Appalachian study areas.

Results

Spatial Extent of the Evergreen Understory Community

As reported in Chastain and Townsend (in review), the forest maps created from the Landsat ETM and topographic data classifications (Figure 3) achieved overall accuracies of 87.1 percent in the Ridge and Valley study area and 82.9 percent on the Allegheny Plateau. Overall accuracy was improved in the Plateau region by incorporating topographic information into the classification process, but inclusion of topographic information increased confusion among winter-green vegetation types in the Ridge and Valley study area because of the intense land-use history in this area (Chastain and Townsend in review). The evergreen understory made up a much greater proportion of the forested area

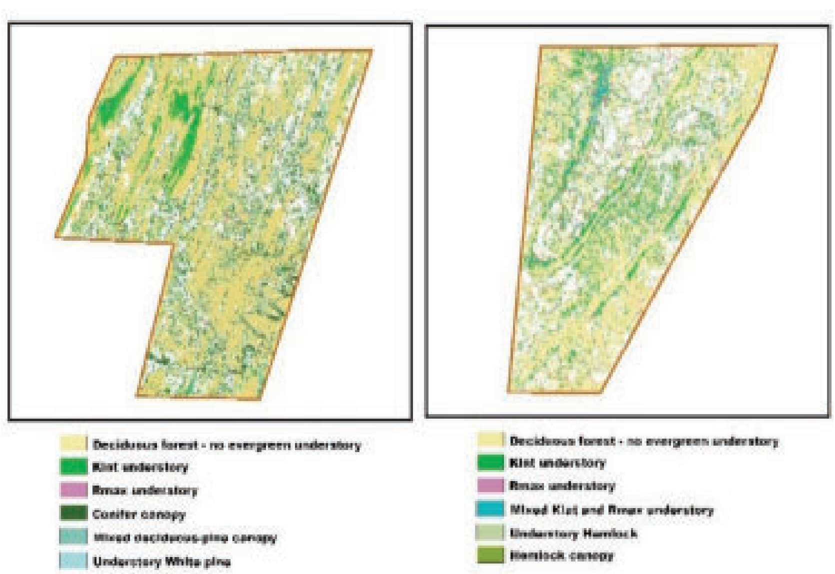

Figure 3.—Maps resulting from the Landsat ETM and topographic data classifications of the Ridge and Valley (left) and Allegheny Plateau (right) study areas.

Table 2.—Results from the hierarchical forest community classification.

Group	Type	Number of Plots Total	Ridge/Valley	Plateau
Oak Forests	chestnut oak dominated	22	17	5
	white oak dominated	8	8	0
	red oak dominated	3	0	3
	mixed oak	20	13	7
Dry Oak Forests		22	22	0
Red Maple/Oak Forests	red maple with red oak	19	6	13
	red maple with chestnut oak	8	0	8
Conifer Forests		6	6	0
Sugar Maple Forests		21	7	14
Kalmia Understory Forests	KLAT with chestnut oak canopy	37	26	11
	KLAT with maple-oak canopy	18	0	18
	KLAT-RMAX with maple/oak canopy	11	0	11
	KLAT w/ red oak canopy	4	0	4
Rhododendron Understory Forests		10	3	7
Hemlock Forests		4	0	4
Total Plots		213	108	105
Evergreen Understory Plots		80		

of the Plateau study area (26.6 percent) compared to the Ridge and Valley study area (6.1 percent) (Figure 3). KLAT-dominated communities were for the most part the only evergreen community present in the Ridge and Valley province, possibly because RMAX's environmental niche is severely constrained by the presence of limestone bedrock in the moister valley locations of this physiographic province, and RMAX seedlings are inhibited by the presence of calcium (Romancier 1970). As a result, RMAX occurs only in steep, narrow stream valleys cut into the sandstone and siltstone ridges in this study area.

Forest Community Classification

The clustering analysis identified 8 major species associations, and a larger number of types based on variations in dominant and overstory species (Table 2). Oak species were dominant or co-dominant in the canopy in 172 out of the 213 plots (with and without evergreen understory layer presence). All 22 of the plots that were classified as 'dry oak' (containing Q. *coccinea* and *Q. velutina*) occurred in the Ridge and Valley province. A total of 80 evergreen understory plots were classified from the plot data, with 29 in the Ridge and Valley, and 51 in the Allegheny Plateau study area. These community classifications were used in subsequent analysis to assess their separability in ordination species-space.

Ordination Results

Nonmetric multidimensional scaling (NMS) showed clear separation among species and vegetation classes (Figure 4). In addition, joint plots with the environmental variables (where the length and direction of the environmental vector is scaled to the strength and direction of the correlation of that variable with the ordination axis) indicate discernable and readily interpretable relationships between species and environmental gradients. First, patterns of species assemblages were distinct between the two physiographic provinces (Figure 4A). In addition, KLAT and RMAX dominated plots are clearly distinct from other vegetation types and themselves in the ordination (Figure 4B). Notably, the Ridge and Valley KLAT plots and the Plateau KLAT plots inhabit distinct space on this plot, with KLAT presence strongly related to gypsy moth defoliation (measured as the cumulative number of years

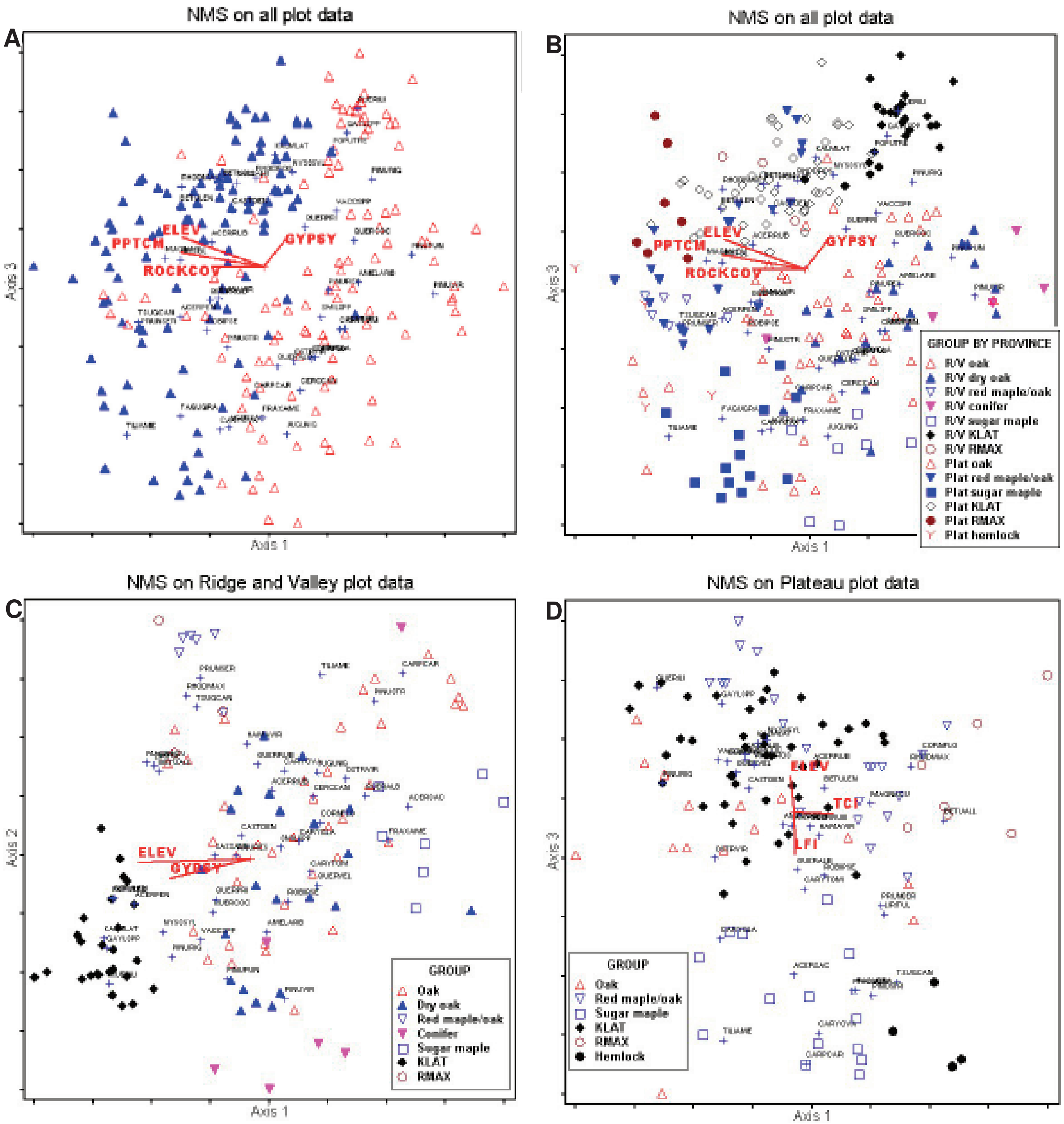

Figure 4.—Joint plots of four separate NMS ordinations of species IV scores and environmental variables. Ordination results of data from all 213 plots symbolized to represent the two study areas are shown in A), with the Plateau plots symbolized as dark triangles, and the Ridge and Valley plots as light triangles. All 213 plots symbolized to indicate the group identified in the community classification (see Table 2) are shown in B), ordination results from the Ridge and Valley plot data are shown in C), and ordination results from Allegheny Plateau plot data are shown in D).

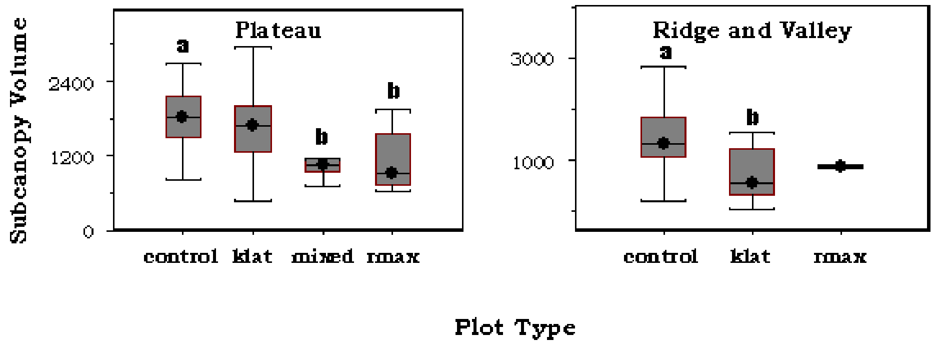

Figure 5.—Box and whisker plots of subcanopy foliar volume for the Allegheny Plateau and Ridge and Valley study areas. The y-axis is a relative measure of cubic meters per 900 meters square, which is the area of a 30-m Landsat TM pixel. Different letters indicate significant differences between classes.

defoliated) in the Ridge and Valley. Examining the Ridge and Valley alone (Figure 4C), the gypsy moth disturbance gradient appears strongly related to the KLAT plots (R with ordination axis 3 = -0.52). The NMS ordination on the Plateau plot data alone suggests the overall importance of topographic gradients in this study area (Figure 4D), as the history of gypsy moth disturbance and land use is less intense. The TCI (wetness index) gradient increases in the direction of the plots containing the moisture-loving RMAX, and the slope gradient decreases in that direction. Similarly, LFI (a gradient of exposed to protected sites) decreases in the direction of the drier KLAT plots. Pearson correlations for TCI with ordination axis 3 = -0.41 and for LFI with axis 1 = -0.42.

ANOVA Results

The ANOVA results indicated that the presence of an evergreen understory was significantly related to a paucity of trees in the midstory (subcanopy) as measured by subcanopy volume in some, but not all understory types in the two study areas (Figure 5). In the Ridge and Valley province, ANOVA results indicated a significant difference in subcanopy volume by plot type ($F = 16.75$, $P < 0.0001$), but while Tukey's multiple comparison test revealed that KLAT plots had a significantly lower subcanopy volume than 'Control' (no evergreen understory) plots, RMAX sites were not significantly different from either the KLAT or 'control' plots. However, the RMAX plots in this province were limited in spatial extent and concentrated in narrow riparian areas where patch width was insufficient to exclude regeneration. ANOVA also indicated that KLAT plots had significantly lower LAI compared to the control and RMAX plots in the Ridge and Valley province ($F = 6.76$, $P = 0.0018$). Further, live BA was significantly lower on KLAT plots compared to both the control and RMAX sites ($F = 18.85$, $P < 0.0001$). Therefore, KLAT communities are demonstrably more open than is typical of other forest types in the region.

Results from the ANOVA on the Allegheny Plateau indicated that the subcanopy volume of the mixed and RMAX plots were significantly lower than the subcanopy volume in the control plots ($F = 4.9$, $P = 0.0034$). Surprisingly, the KLAT plots and control plots were not significantly different with respect to subcanopy volume (Figure 5). Although not clear from the data, KLAT communities may be patchier on the Plateau. The ANOVA results also indicated that KLAT plots had a significantly lower average LAI than RMAX plots ($F = 5.64$, $P = 0.0014$), but was not significantly lower than the average LAI on the control plots. No significant BA differences were noted between the Plateau plot types.

Discussion

The composition and structure of forests in the central Appalachian highlands have developed as a result of climate, topography, land use, and disturbance. However, disturbance and land use tend to complicate the association between vegetation patterns and the direct and resource gradients that influence forest composition. The successful mapping of the evergreen understory communities in these two adjacent but dissimilar study areas in the central Appalachian highlands has yielded a clearer understanding of their spatial extent and pattern of occurrence. Ordination of plot data showed that indirect gradients related to environmental history were important for characterizing the distribution of KLAT and RMAX. In the Ridge and Valley, gypsy moth defoliation opened up the subcanopy light environment permitting the development of dense stands of *Kalmia*, whereas on the Plateau, climate and terrain-related gradients distinguished KLAT and RMAX from each other and forests without an evergreen understory layer. Finally, the data indicate that the evergreen understory significantly affects the structural characteristics of forest stands containing dense KLAT or RMAX. Although plot level studies performed in other locations in the Appalachians confirm this result, this research provides data to assess on a regional scale the spatial implications of understory communities on overall forest structure, stand dynamics, and regeneration. The dynamics of KLAT and RMAX are therefore a central component to central Appalachian forest communities.

The overarching goal of this research is to examine the prevalence, ecological impacts and potential future influence of dense evergreen understory coverage in the central Appalachian highland forests. Further work to address this entails the examination of the temporal dynamics of KLAT- and RMAX-dominated understory communities over a 16 year period using remote sensing imagery and assessing via simulation models the importance of these understory communities with respect to carbon sequestration and nutrient dynamics on a landscape scale. Ultimately this research will provide the basis for informed management decisions and adaptive management strategies in Appalachian forests.

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