

Variation in Soil and Forest Floor Characteristics Along Gradients of Ericaceous, Evergreen Shrub Cover in the Southern Appalachians

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ABSTRACT Ericaceous shrubs can influence soil properties in many ecosystems. In this study, we examined how soil and forest floor properties vary among sites with different ericaceous evergreen shrub basal area in the southern Appalachian mountains. We randomly located plots along transects that included open understories and understories with varying amounts of *Rhododendron maximum* (rosebay rhododendron) and *Kalmia latifolia* (mountain laurel) at three sites. The three sites were a mid-elevation ridge, a low-elevation cove, and a high-elevation southwest-facing slope. Basal area of *R. maximum* was more correlated with soil properties of the forest floor than was *K. latifolia*. Increasing *R. maximum* basal area was correlated with increasing mass of lower quality litter and humus as indicated by higher C:N ratios. Moreover, this correlation supports our prediction that understory evergreen shrubs may have considerable effect on forest floor resource heterogeneity in mature stands.

INTRODUCTION Vegetation is one of the primary factors contributing to soil genesis (Boettcher and Kalisz 1990). Many studies have shown the effects of individual tree species on soil chemical and physical properties (Zinke 1962, Challinor 1968, Chastain et al. 2006, Boerner and Koslowsky 1989, Boettcher and Kalisz 1990, Pelletier et al. 1999). Woody species may affect soil properties by redistributing nutrients within the rooting zone (Boettcher and Kalisz 1990) and by the synthesis and input of organic material in the form of root exudates and decomposing litter (Boerner and Koslowsky 1989). Additionally, litter quality may influ-

ence decomposition and nutrient turnover rates. For example, litter of species with higher lignin content has slower decomposition rates (Hobbie et al. 2006).

Ericaceous plants, in particular, influence soil properties by reducing soil enzyme activities and slowing nutrient cycling (Bloom and Mallik 2006, Chastain et al. 2006, Joannis et al. 2007). This influence is primarily a result of litter quality and a large concentration of polyphenolic compounds (Wurzberger and Hendrick 2007). These phenolic compounds often bind with organic materials in the soil preventing or slowing their decomposition (Joannis et al. 2007, Wurzberger and Hendrick 2007), reducing rates of nutrient mineralization (Straker 1996, Northup et al. 1998). Many ericaceous plants influence nutrient availability in cold-temperate or boreal regions that are nitrogen limited (Nilsson and Wardle 2005); however, ericaceous vegetation can also alter nutrient cycling in warm

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temperate forests that have high nitrogen availability (Gilliam et al. 2005, Wurzbarger and Hendrick 2007). Evergreen ericaceous plants may further exacerbate low nutrient availability by sequestering nutrients in their foliage (Thomas and Griegel 1976, Monk et al. 1985). These evergreens are usually better adapted for conserving limited nutrients than other growth forms through slower growth and re-utilization of existing foliar nutrients (Chapin 1980).

Rhododendron maximum and *Kalmia latifolia* are ericaceous evergreen understory shrubs that are important components of forests in the southern Appalachians (Radford et al. 1964, Monk et al. 1985) and, where they occur, generally dominate the understory. Thickets of these two species cover about 12 million hectares in eastern North America (Dobbs 1998). In one north-facing watershed at the Coweeta Hydrologic Laboratory in North Carolina, *R. maximum* and *K. latifolia* made up 7.4 and 5.1%, respectively, of total basal area (Day et al. 1988). Furthermore, the extent of *R. maximum* cover has been increasing over the past one hundred years due to changes in forest composition and structure (McGinty 1976, Monk et al. 1985, Phillips and Murdy 1985) brought on by changes in forest management strategies, fire control, and invasive plant pathogens. Several studies have shown that high densities of *R. maximum* interfere with canopy seedling establishment (Monk et al. 1985, Clinton et al. 1994, Beckage et al. 2000, Lei et al. 2002, Beckage and Clark 2003, Beckage et al. 2005, Beier et al. 2005). While low light under *R. maximum* thickets is the primary factor reducing seedling establishment (Clinton et al. 1994, Lei et al. 2002, Beier et al. 2005), soil properties, such as reduced nutrient availability and increased litter and humus depth, also play a role (Clinton and Vose 1996, Nilsen et al. 2001, Lei et al. 2006). Therefore, it is likely that thickets of ericaceous evergreen shrubs in the understory influence forest floor and soil resource heterogeneity.

Studies have shown reduced concentrations of key nutrients (e.g., Ca, Mg, K), lower pH, and slower N-mineralization rates on sites with *R. maximum* relative to sites with deciduous cover (Boettcher and Kalisz 1990, Nilsen et al. 2001). Furthermore, both leaves (Yang and Wang 1978) and roots (Peterson et al. 1980) of *R. maximum* are rich in phenolic

compounds (Vance et al. 1986). These factors are thought to give evergreen shrubs a competitive advantage over their deciduous counterparts because they are able to draw down resources to values inappropriate for their deciduous competitors (Tilman 1982, Bloom and Mallik 2006). It is critical to understand the effect of evergreen shrubs on forest floor resources because those resources have an important influence on canopy tree recruitment and long term forest dynamics.

Our objectives were to investigate the variation of forest floor and soil properties in forest sites with a mosaic of different shrub cover in southern Appalachian forests. With increasing shrub cover we predicted: 1) litter and humus mass would increase due to an accumulation of recalcitrant litter from ericaceous shrubs, 2) litter and humus quality would decrease (in terms of nitrogen concentration and C:N ratios), 3) pH and nutrient availability would decrease, and, 4) these changes to be greater in plots with *R. maximum* than in plots with *K. latifolia*.

MATERIALS AND METHODS

Study Sites

This study took place on three sites in the Nantahala National Forest in the Blue Ridge Physiographic Province of southwestern North Carolina. The first site, (LE—low elevation), was located on a northwest aspect at an elevation of 750 m in a mixed oak-hickory forest (*Quercus rubra*, *Q. coccinea*, *Q. alba*, *Q. falcata*, *Carya glabra* and *Carya tomentosa*) on an Evard-Cowee soil series, a fine-loamy, oxidic, mesic Typic Hapludult (United States Department of Agriculture 2007). Nomenclature follows Radford et al. (1964). The second site, (ME—middle elevation), was located on an east-northeast aspect at an elevation of 1,180 m in a mixed upland oak forest (*Q. prinus* and *Q. rubra*) with a significant *Acer rubrum* component on a Plott soil series, a coarse-loamy, mixed, mesic Typic Haplumbrept (United States Department of Agriculture 2007). These two sites are both located within the basin of the Coweeta Hydrologic Laboratory (35°03'N, 83°25'W). The Coweeta Basin is typified by marine, humid forests with ample precipitation (Swank and Crossley 1988). The third site (HE—high elevation) was located approximately 30 km northwest from Coweeta in the Wine Springs Creek Ecosystem Management Project Area (35°11'N,

83°36'W; see Swank and Culpepper 1992). This study site was on a south-southwest aspect at an elevation of 1,340 m in a mixed upland oak forest with large component of *A. rubrum* and *Tsuga canadensis* (see Elliott and Hewitt 1997) for a complete vegetation description of this area), on a Plott soil series similar to ME described above (United States Department of Agriculture 2007). All three sites contained varying amounts of *R. maximum* and *K. latifolia* spread throughout the site as well as areas void of ericaceous evergreen shrub understory. These sites were chosen to represent characteristic forest types in the southern Appalachian region and to span a range of geographic variability within the region of the Nantahala National Forest.

Average annual precipitation for the LE site is 1,800 mm, distributed evenly throughout the year. Average monthly temperatures range from 3°C in January to 22°C in July. The climate regime at the more elevated ME site is somewhat wetter and cooler. The HE site is somewhat higher in elevation (approx. 150 m) than the ME site, yet average annual precipitation has been less (approx. 20%). During this period of record (1994–2004), much of the precipitation was dominated by relatively isolated events with several years of precipitation deficits (Coweeta LTER, http://coweeta.ecology.uga.edu/ecology/ecology_data.html). Although overall month-to-month variation was similar across sites, HE is 30 km distant from ME, so this discrepancy in total rainfall may have been the result of the stochastic nature of the weather patterns during that period. Similarly, average daily temperature was almost 10% higher at HE than ME, which may have been due to the greater total direct solar radiation on the south facing HE.

Plot Layout and Vegetation Survey

In 2000, we installed four parallel transects at LE and ME and three transects at HE running along the contour. Along each sampling transect, we randomly located fifteen 2 × 2 m plots (20 at HE) placed 8–15 m apart, for 60 plots per site. Plot transects passed through a mosaic of forest vegetation including open and shrub-influenced understories, such that shrub density among plots ranged from absent to dense thicket. These plots were established as part of a larger study investigating the survival and growth of *Quercus* and *Pinus* seedlings planted in them (Beier et al.

2005). All plots within each site were contained in an area of 1.5 ha (300 m × 50 m). Basal diameter on all stems of *R. maximum* and *K. latifolia* within a 2.5 m radius of plot center was measured and basal area was summed for each plot. To characterize the canopy composition at each study site, we identified and measured diameter at breast height (dbh) of all stems > 10 cm dbh within a radius of 5 m from plot center. Additionally, we sampled the subcanopy (stem dbh > 2.5 cm and < 10 cm) within a radius of 2.5 m from plot center.

Soil and Forest Floor Sampling

From each 2 × 2 m plot on all sites, five mineral soil samples were taken in June 2000 to a depth of 10 cm and composited for nutrient analysis. Soil pH, cation and anion concentrations were determined by the Soil Testing Laboratory at Virginia Tech using inductively coupled plasma mass spectroscopy (Thermo Jarrell Ash Corp., model ICAP 61, Franklin, Massachusetts). Additionally, four measurements of soil depth were taken and averaged in each plot using a thin diameter metal rod inserted into the soil until bedrock was encountered. Organic soil samples were taken in each plot corner for four subsamples per plot using a 10 cm diam PVC core. The organic soil was divided into litter defined as the unconsolidated material above the fermentation layer (O_i), and the fermentation and humus ($O_a + O_e$) layers combined (hereinafter referred to as the humus layer). The four individual subsamples of litter and humus were pooled separately at the plot level, oven dried at 55°C and weighed to the nearest 0.01 g. Estimates of litter and humus thickness were made at five locations on each plot and averaged for mean thickness. Litter and humus samples were ground and analyzed separately for carbon and nitrogen concentration on a Perkin-Elmer 2400 CHN Elemental Analyzer. These concentrations were combined with litter and humus weight to estimate total litter and humus carbon and nitrogen pools.

Statistical Analysis

All soil and forest floor characteristics were compared among sites ($n = 60$ plots per site) using Analysis of Variance (ANOVA: PROC GLM, SAS Institute 1994). Because many of

Table 1. Total species basal area (m^2/ha) calculated from 60 plots at each site. Values are for basal area at breast height (1.3 m) except for *Kalmia latifolia* and *Rhododendron maximum*, which represent basal area at ground level. Nomenclature follows Radford et al. (1964)

Species Basal Area (m^2/ha)	LE	ME	HE
<i>Kalmia latifolia</i> L.	9.956	2.399	2.799
<i>Rhododendron maximum</i> L.	5.140	6.051	3.840
<i>Acer pensylvanicum</i> L.	0.063	0.010	0
<i>Acer rubrum</i> L.	2.451	5.290	6.679
<i>Amelanchier arborea</i> (Michx. f.) Fernald	0.565	1.454	0
<i>Betula lenta</i> L.	0.299	1.183	0.291
<i>Castanea dentata</i> Sudworth	0	0.106	0.207
<i>Carya glabra</i> (Mill.) Sweet	1.308	2.152	3.314
<i>Carya tomentosa</i> (Lam.) Nutt.	1.963	0	0.123
<i>Clethra acuminata</i> Michx.	0	0.038	0
<i>Cornus florida</i> L.	0.233	0	0
<i>Fagus grandifolia</i> Ehrh.	0.341	0	0
<i>Halesia carolina</i> L.	0	0	0.103
<i>Hamamelis virginiana</i> L.	0.169	1.384	0.068
<i>Ilex montana</i> Torr & A. Gray	0	0.019	0.016
<i>Liriodendron tulipifera</i> L.	6.393	0	0
<i>Magnolia acuminata</i> L.	0.012	0	0
<i>Magnolia fraseri</i> Walter	0.155	0.033	0
<i>Nyssa sylvatica</i> Marshall	0.741	0.535	0.640
<i>Oxydendrum arboreum</i> (L.) DC.	2.326	1.523	0.066
<i>Pinus strobus</i> L.	0.012	0	0
<i>Pyrularia pubera</i> Michx.	0	0.019	0.023
<i>Quercus alba</i> L.	5.661	4.278	2.509
<i>Quercus coccinea</i> Münchh.	2.359	0	0
<i>Quercus falcata</i> Michx.	4.766	0	0.358
<i>Quercus prinus</i> L.	0.369	12.630	6.911
<i>Quercus rubra</i> L.	0.608	8.687	4.927
<i>Quercus velutina</i> Lam.	1.030	0.094	0
<i>Rhododendron calendulaceum</i> (Michx.) Torrey	0.011	0.339	0.308
<i>Robinia pseudoacacia</i> L.	0.126	0.471	1.250
<i>Tsuga canadensis</i> Carrière	0.187	0.140	5.832
<i>Vaccinium constablaei</i> A. Gray	0	0.069	0.016

the soil properties within each site are likely autocorrelated, we used Principal Components Analysis (PCA) to extract the main components of variability in soil nutrient parameters (PC-ORD; McCune and Medford 1999). This analysis was done for both the organic (8 factors) and mineral (14 factors) soil layers. We then used the extracted PCA axis (with eigenvalues greater than 1) scores for each plot as synthetic variables for each plot in Spearman correlations (PROC COR, SAS Institute 1994) with the total basal area of each shrub and dominant overstory vegetation (Bloom and Mallik 2006). Eigenvectors of each PCA axis were considered influential if they had values ± 0.150 . Canopy basal area components used in this analysis included *Acer rubrum*, pooled basal area from both *Carya* species, *Liriodendron tulipifera*, *Quercus* species both individually and with basal area pooled across species, and *Tsuga canadensis*.

RESULTS

Vegetation Survey

Two of the three sites (ME and HE) had similar overstories both in terms of species composition and distribution based on total basal area (Table 1). With the exception of greater total basal area in *Acer rubrum* and *Tsuga canadensis* and, to a lesser extent, the nitrogen fixing *Robinia pseudoacacia*, the distribution of total basal area at ME and HE were very similar. On the other hand, LE was located on a lower slope and showed a much more heterogeneous distribution that emphasized drier site species such as *Oxydendron arboreum*, *Carya tomentosa* (= *alba*), *Quercus coccinea*, and *Q. falcata* on the upper transects. However, due to a slightly more northerly aspect than other sites, *Liriodendron tulipifera* was present in greater abundance at LE compared with ME and HE. In addition, *Q. prinus* and *Q. rubra* had the highest basal area of all species at ME and HE but were substantially less

Table 2. Comparisons of forest floor properties among sites (LE: a low elevation cove site; ME: a mid-elevation ridge; and HE: a high-elevation south-west facing slope). Means \pm 1 SE are presented from 60 plots per site. Site means within a property having different superscripts are significantly different ($p < 0.05$)

Characteristic	LE	ME	HE
Litter mass (g/m ²)	8,761 \pm 350 ^b	13,418 \pm 530 ^a	8,366 \pm 492 ^b
Litter depth (cm)	5.8 \pm 0.2 ^a	5.4 \pm 0.2 ^a	4.7 \pm 0.2 ^b
Humus mass (g/m ²)	33,047 \pm 1,654 ^b	45,536 \pm 2,825 ^a	23,413 \pm 2,160 ^c
Humus Depth (cm)	1.81 \pm 0.1 ^b	4.6 \pm 0.3 ^a	2.6 \pm 0.3 ^b
Litter N (%)	1.1 \pm 0.0 ^b	1.4 \pm 0.0 ^a	1.4 \pm 0.0 ^a
Litter N total (kg/ha)	98.9 \pm 3.9 ^b	181.7 \pm 7.2 ^a	112.8 \pm 6.0 ^b
Litter C (%)	44.1 \pm 0.3 ^b	48.5 \pm 0.2 ^a	48.1 \pm 0.4 ^a
Litter C total (kg/ha)	3,879.9 \pm 159.0 ^b	6,518.3 \pm 265.0 ^a	4,047.6 \pm 251.0 ^b
Litter C:N	39.4 \pm 0.7 ^a	36.3 \pm 0.7 ^b	35.6 \pm 0.7 ^b
Humus N (%)	0.8 \pm 0.0 ^b	1.4 \pm 0.0 ^a	1.3 \pm 0.0 ^a
Humus N total (kg/ha)	268.0 \pm 14.6 ^b	647.2 \pm 38.8 ^a	333.7 \pm 34.4 ^b
Humus C (%)	24.5 \pm 1.1 ^a	42.3 \pm 0.8 ^b	37.2 \pm 1.5 ^c
Humus C total (kg/ha)	7,872.3 \pm 503.4 ^b	19,602.8 \pm 1,427.6 ^a	9,712.0 \pm 1,063.3 ^b
Humus C:N	28.9 \pm 0.5 ^{ab}	29.5 \pm 0.5 ^a	27.7 \pm 0.5 ^b

frequent at LE and contributed very little to total basal area on that site. Total *Rhododendron maximum* basal area among the three sites was similar; however, *Kalmia latifolia* basal area was highest at LE and similar between ME and HE.

Forest Floor and Soil Properties—Site Differences

Forest floor and soil properties differed considerably among sites. The ME site had significantly higher litter and humus mass than LE or HE, as well as greater total nitrogen and carbon in the litter and humus layers (Table 2). Litter C:N ratios were significantly lower at ME and HE than at LE, and humus C:N ratio was significantly greater at ME compared with HE (Table 2). Soil pH differed significantly among sites; it was lowest at ME,

intermediate at HE and highest at LE. Certain soil cation concentrations were significantly highest (Mg, Fe), or tended to be highest (K) at ME, but there was no consistent trend for soil cation concentrations among sites (Table 3).

Principal Components Analysis and Correlation Within Sites

In the organic soil layer at LE, principal components analysis defined three axes that accounted for 75% of the total variance (Table 4). Axis 1 was associated with decreased values in five soil parameters (humus N content, humus C content, litter C content, litter N content and litter mass) and increased humus mass. Axis 2 was associated primarily with increased litter C:N, humus C:N, litter mass and humus mass and decreased litter N content. Axis 3 was associated with decreased

Table 3. Comparisons of soil properties among sites (LE: a low elevation cove site; ME: a mid-elevation ridge; and HE: a high-elevation south-west facing slope). Means \pm 1 SE are presented from 60 plots per site. Site means within a property having different superscripts are significantly different ($p < 0.05$)

Characteristic	LE	ME	HE
Soil depth (cm)	40.9 \pm 1.0 ^a	29.2 \pm 1.2 ^b	24.82 \pm 1.1 ^c
Soil N (%)	0.1 \pm 0.0 ^b	0.2 \pm 0.0 ^a	0.2 \pm 0.0 ^a
Soil C (%)	2.6 \pm 0.1 ^c	4.0 \pm 0.3 ^b	5.1 \pm 0.3 ^a
pH	4.9 \pm 0.0 ^a	4.7 \pm 0.0 ^c	4.8 \pm 0.0 ^b
Ca (mg/L)	50.5 \pm 2.1 ^b	56.5 \pm 3.7 ^{ab}	66.7 \pm 3.8 ^a
Mg (mg/L)	18.2 \pm 0.7 ^b	20.9 \pm 1.1 ^a	16.4 \pm 0.6 ^b
P (mg/L)	0.4 \pm 0.2 ^a	0.3 \pm 0.1 ^a	0.8 \pm 0.2 ^a
K (mg/L)	20.8 \pm 0.7 ^b	34.0 \pm 1.1 ^a	30.8 \pm 1.2 ^a
Mn (mg/L)	3.0 \pm 0.2 ^b	1.8 \pm 0.4 ^c	4.6 \pm 0.3 ^a
Zn (mg/L)	0.8 \pm 0.0 ^b	0.8 \pm 0.0 ^b	0.9 \pm 0.0 ^a
Fe (mg/L)	16.1 \pm 0.6 ^c	28.4 \pm 1.5 ^a	21.5 \pm 1.3 ^b
Al (mg/L)	380.4 \pm 7.9 ^b	693.5 \pm 19.4 ^a	698.0 \pm 22.2 ^a
Cu (mg/L)	1.1 \pm 0.0 ^a	0.4 \pm 0.0 ^b	0.3 \pm 0.0 ^b
B (mg/L)	0.1 \pm 0.0 ^a	0.1 \pm 0.0 ^a	0.1 \pm 0.0 ^a

Table 4. Principal components analysis (PCA) axes generated from the organic soil layer components at three sites in the southern Appalachian Mountains. PCA axes with eigenvalues < 1 are not included. Eigenvectors for each soil component within each axis are presented. High magnitude eigenvector values (± 0.150 or larger) for soil parameters indicate a strong influence on the PCA axis

Parameters	LE			ME			HE	
	PCA-1	PCA-2	PCA-3	PCA-1	PCA-2	PCA-3	PCA-1	PCA-2
Eigenvalue	2.62	2.19	1.20	3.21	1.86	1.23	3.94	1.48
Explained variance (%)	32.7	27.4	15.0	40.1	23.7	15.4	49.3	18.5
Cumulative variance explained (%)	32.7	60.1	75.1	40.1	63.8	79.2	49.3	67.7
Litter mass	-0.160	0.355	0.056	-0.277	-0.329	0.208	-0.322	0.055
Litter N Content	-0.242	-0.537	0.304	0.463	-0.196	0.389	-0.300	-0.581
Litter C Content	-0.440	0.143	-0.147	-0.044	-0.292	0.612	-0.255	-0.089
Litter C:N	-0.007	0.614	-0.322	-0.486	0.170	-0.238	-0.389	0.468
Humus mass	0.270	0.187	0.610	-0.373	0.081	0.453	-0.394	0.105
Humus N content	-0.567	-0.040	-0.020	0.005	-0.665	-0.326	-0.336	-0.516
Humus C content	-0.570	0.096	0.211	-0.338	-0.517	-0.155	-0.433	-0.350
Humus C:N	-0.066	0.377	0.602	-0.466	0.155	0.199	-0.367	-0.185

litter C:N and increased values in four organic soil parameters (humus mass, humus C:N, litter C:N and humus C content). *Rhododendron maximum* basal area was negatively correlated with axis 1 and positively correlated with axes 2 and 3 (Table 5). As *R. maximum* basal area increased, so did litter mass, litter C:N, humus mass and humus C:N. *Acer rubrum* basal area was positively correlated ($r_s = 0.337$, $p = 0.008$) with axis 1 and negatively correlated ($r_s = -0.270$, $p = 0.035$) with axis 2. *Kalmia latifolia* was not correlated with any soil organic axis at LE.

At ME the three axes generated for the organic soil accounted for 79.2% of the

variance (Table 4). Axis 1 was associated with decreased values in five soil parameters (litter C:N, humus C:N, humus mass, humus C content and litter mass) and with increased litter N content. Axis 2 was associated with decreased values in five soil parameters (humus N content, humus C content, litter mass, litter C content and litter N content) and increased litter and humus C:N. Axis 3 was associated with decreased humus N content, litter C:N and humus C content and with increased values in five soil parameters (litter C content, humus mass, litter N content, litter mass and humus C:N). *Rhododendron maximum* basal area was negatively

Table 5. Correlations between principal components axes (PCA) and basal area of *Kalmia latifolia* and *Rhododendron maximum* at three sites (LE, ME, and HE) in the southern Appalachians. Spearman correlation coefficient (r_s) and p-values (p) are presented. Bold values are significant at the $p < 0.05$ level

Site/Vegetation		Organic			Mineral		
		PCA-1	PCA-2	PCA-3	PCA-1	PCA-2	PCA-3
LE							
<i>Kalmia</i>	$r_s =$	0.04	0.02	0.21	0.15	-0.02	0.13
	p =	0.76	0.86	0.11	0.25	0.90	0.33
<i>Rhododendron</i>	$r_s =$	-0.25	0.32	0.52	-0.14	0.36	-0.05
	p =	0.05	0.01	0.00	0.30	0.01	0.69
ME							
<i>Kalmia</i>	$r_s =$	0.04	-0.19	0.14	0.05	-0.18	-0.33
	p =	0.76	0.14	0.30	0.71	0.16	0.01
<i>Rhododendron</i>	$r_s =$	-0.44	0.36	-0.07	0.07	-0.01	-0.03
	p =	0.00	0.00	0.60	0.62	0.95	0.85
HE							
<i>Kalmia</i>	$r_s =$	0.36	-0.11	N/A	0.10	-0.34	-0.16
	p =	0.01	0.42		0.45	0.01	0.22
<i>Rhododendron</i>	$r_s =$	-0.64	-0.07	N/A	-0.11	0.70	0.30
	p =	0.00	0.61		0.42	0.00	0.02

Table 6. Principal components analysis (PCA) axes generated from the mineral soil layer components at three sites in the southern Appalachian Mountains. PCA axes with eigenvalues < 1 are not included. Eigenvectors for each soil component within each axis are presented. High magnitude eigenvector values (± 0.15 or larger) for soil parameters indicate a strong influence on the PCA axis

Parameters	LE			ME			HE		
	PCA-1	PCA-2	PCA-3	PCA-1	PCA-2	PCA-3	PCA-1	PCA-2	PCA-3
Eigenvalue	3.46	2.66	2.07	5.03	2.49	1.83	4.77	2.50	1.76
Explained variance (%)	24.70	18.98	14.76	35.96	17.81	13.10	34.04	17.83	12.54
Cumulative variance explained (%)	24.70	43.68	58.44	35.96	53.77	66.87	34.04	51.87	64.41
Soil Depth	-0.02	-0.02	-0.37	0.10	0.01	-0.26	-0.04	-0.13	0.16
pH	-0.00	-0.48	-0.14	0.09	-0.15	0.54	0.12	-0.54	-0.14
Ca	-0.17	-0.43	0.02	-0.37	-0.09	0.06	-0.24	-0.42	-0.23
Mg	-0.17	-0.40	0.16	-0.35	-0.28	0.03	-0.37	-0.16	-0.22
P	0.05	0.08	0.33	-0.33	-0.24	-0.06	-0.17	-0.05	-0.18
K	-0.35	0.08	0.11	-0.36	0.01	0.00	-0.35	-0.05	-0.30
Mn	-0.24	0.10	0.45	-0.22	-0.25	0.30	-0.32	-0.17	-0.10
Zn	-0.36	-0.22	0.23	-0.38	-0.02	-0.24	-0.39	0.18	0.00
Fe	-0.18	0.29	0.46	-0.12	-0.04	-0.51	-0.14	0.47	-0.03
Al	-0.34	0.30	-0.19	0.00	0.52	0.23	0.07	0.09	0.18
Cu	-0.09	0.31	-0.17	-0.04	-0.43	0.22	-0.20	-0.22	0.58
B	-0.30	-0.27	0.06	-0.17	0.24	0.33	-0.22	-0.23	0.58
Soil N content	-0.44	0.08	-0.29	-0.35	0.35	0.00	-0.35	0.23	0.10
Soil C content	-0.44	0.07	-0.29	-0.34	0.36	0.09	-0.37	0.19	0.05

correlated with axis 1 and positively correlated with axis 2 (Table 5). As *R. maximum* basal area increased so did litter and humus mass, litter and humus C:N, litter C and litter N content while humus C and N contents decreased. *Acer rubrum* was negatively ($r_s = -0.367$, $p = 0.004$) and *Carya* spp. were positively ($r_s = 0.378$, $p = 0.003$) correlated with axis 1, while *L. tulipifera* and *Q. prinus* were both positively correlated with axis 2. *Kalmia latifolia* was not correlated with any soil organic axis at ME.

At HE there were only two axes generated from the organic soil parameters accounting for 67.7% of the total variance (Table 4). Axis 1 was associated with decreased values in all organic soil parameters (humus C content, humus mass, litter C:N, humus C:N, humus N content, litter mass, litter N content, and litter C content). Axis 2 was associated with decreased values in four soil parameters (litter N content, humus N content, humus C content, humus C:N) and increased litter C:N ratio. *Kalmia latifolia* basal area was positively correlated with axis 1 while *Rhododendron maximum* basal area was negatively correlated with axis 1. *Carya* spp. were positively ($r_s = 0.359$, $p = 0.005$) while *T. canadensis* was negatively ($r_s = -0.490$, $p < 0.001$) correlated with axis 1. No vegetation

component was correlated with axis 2 (Table 5).

In the mineral soil data from LE, three PCA axes accounted for 58.4% of the total variance (Table 6). Axis 1 was associated decreased soil N and C content and concentration of several soil cations (Zn, K, Al, B, Mn, Fe, Ca and Mg), however, no shrub component was correlated with this axis. Axis 2 was associated with decreased soil pH and concentration of several soil cations (Ca, Mg, B and Zn) and increased concentrations of other soil cations (Cu, Al and Fe). This axis was positively correlated with *R. maximum* basal area suggesting that as basal area increased, pH decreased with the associated changes in soil cations. *Quercus rubra* was negatively ($r_s = -0.350$, $p = 0.007$) correlated with axis 1 and positively ($r_s = 0.396$, $p = 0.002$) with axis 2. Axis 3 was associated with decreased soil depth, soil N, soil C content, Al and Cu concentration and increased concentrations of other cations (Fe, Mn, P, Zn and Mg). Axis 3 was not correlated with any plant component. There was no relationship between *K. latifolia* basal area and any PCA axis in the mineral soil at LE.

At ME the three axes derived from the mineral soil accounted for 66.9% of the total variance (Table 6). Axis 1 was associated with

decreased soil N content, soil C content and concentration of several soil cations (Zn, Ca, K, Mg, P, Mn and B). However, this axis was not correlated with any vegetation component. Axis 2 was associated with increased soil C content, soil N content, Al concentration and B concentration and decreased concentrations of Cu, Mg, P and Mn. This axis was not correlated to either shrub component, but was negatively correlated with *L. tulipifera* basal area ($r^2 = -0.344$, $p = 0.007$). Axis 3 was associated with decreased Fe concentration, Zn concentration and soil depth and increased soil pH and concentrations of B, Mn, Al and Cu. This axis was negatively correlated with *K. latifolia* basal area (Table 5).

The three axes from the mineral soil at HE accounted for 64.4% of the total variance (Table 6). Axis 1 was associated with decreased soil C and N content and concentrations of several soil cations (Zn, Mg, K, Mn, Ca, B and Cu) but was not correlated with any vegetation component. Axis 2 was associated with decreased soil pH and concentration of several cations (Ca, B, Cu, Mn and Mg) and increased Fe concentration, Zn concentration, soil N content and C content. This axis was positively correlated with *R. maximum* and negatively correlated with *K. latifolia* (Table 5) and *Carya* spp. basal area ($r_s = -0.297$, $p = 0.021$). Axis 3 was associated with decreased concentrations of K, Ca, Mg and P and increased concentrations of B, Cu, Al and soil depth. This axis was positively correlated with *R. maximum* basal area (Table 5).

DISCUSSION The southern Appalachian forest is dominated by broadleaved deciduous trees, which can exert considerable influence over the chemical and physical make up of the forest floor (Zinke 1962, Challinor 1968, Boerner and Koslowsky 1989, Boettcher and Kalisz 1990, Pelletier et al. 1999). The effect of evergreen understory shrub species on these properties is less well understood. We expected litter and humus depth to increase and that the quality of these forest floor components would decrease with increasing shrub basal area. Ericaceous evergreen shrubs are known to have low-nutrient, recalcitrant litter (Wurzburger and Hendrick 2007). Moreover, we expected that these differences in litter and humus would be associated with a lower soil pH and depleted soil nutrient resources.

Results from the Principal Components Analysis and correlation suggest that increasing *Rhododendron maximum* basal area is associated with increasing litter and humus mass and C:N ratios at all sites, as predicted. *Rhododendron maximum* basal area was associated with decreasing litter N content at all sites, but was variably associated with humus N. At LE and HE, *R. maximum* basal area was associated with increasing humus C and N content, while at ME it was associated with decreasing humus C and N. One might expect humus C content and C:N to increase with increasing inputs of *R. maximum* litter to the forest floor. High phenolic compound concentration in *R. maximum* litter may slow its decomposition (Joanisse et al. 2007, Wurzburger and Hendrick 2007) and reduce rates of nutrient mineralization (Straker 1996, Northup et al. 1998), thus resulting in accumulation of C and increase in C:N ratio in the humus layer. Additionally, much of the N in the humus layer may be bound in recalcitrant organic compounds and unavailable to plants. The site discrepancy in this relationship may be due to differences in overstory species composition or microclimatic variables that affect decomposition and nutrient mineralization.

Kalmia latifolia basal area was not correlated with any organic forest floor component at LE or ME, but was correlated with decreased litter and humus mass and litter and humus C:N ratios at HE. The opposite correlations of *R. maximum* and *K. latifolia* at HE may be the result of competition or niche partitioning between the species. Generally, *K. latifolia* occurs on drier, more well-drained sites than *R. maximum*. Other vegetation components were associated with organic soil PCA axes at some sites, but these were not universal across all sites and no discernable patterns were observed for other species in our analyses.

The variation in organic soil properties with increased *R. maximum* basal area illustrate the effect that slow decomposition of recalcitrant litter has on C accumulation. Much of the litter beneath *R. maximum* retained large quantities of C in recalcitrant forms raising the C:N ratio of that layer compared with the other understory vegetation conditions. Although the sclerophyllous character of *K. latifolia* litter is comparable with *R. maximum* (Thomas and Grigal 1976), there tended to be relatively less *K. latifolia* leaf litter on the forest

floor on *K. latifolia* dominated sites. In contrast, the litter layer beneath *R. maximum* consisted predominantly of *R. maximum* leaf litter (pers. obs.). Because of this lower litter accumulation, *K. latifolia* had less influence on C and N pools in the forest floor than *R. maximum*.

Rhododendron maximum basal area was correlated with decreased soil pH, Ca and Mg concentrations and increasing Al, Fe and Cu concentrations at LE and HE. *Kalmia latifolia* basal area was correlated with decreased soil pH and increased Fe concentrations at ME and HE. Other vegetation components that were associated with soil properties included *Quercus rubra* associated with increased soil C and N content at LE, *Liriodendron tulipifera* associated with increased soil pH and Ca and Mg concentration with decreased Al, Fe and Cu concentrations at LE, and *Carya* spp. associated with increased soil pH and Ca concentration and decreased Al concentration.

Soil chemical properties are known to vary with microsites associated with the bases of different tree species (Boerner and Koslowski 1989, Hobbie et al. 2006). Surface soil chemistry around tree bases of some species may differ significantly from soils around other tree species. This influence may extend away from tree bases due to differences in chemistry as well as volume of stemflow (Zinke 1962, Gersper and Holowaychuk 1970, Crosier and Boerner 1984), differential rates of root exudates, or decay of leaf masses with different nutrient concentrations or amounts of defensive and structural compounds (e.g., tannins, lignin). During sampling, we did not attempt to avoid tree bases so that to some degree our results may have been influenced by local variation due to stemflow volume and chemistry. However, the influence of recalcitrant *R. maximum* litter seems to override this influence in some locations. The strongest influence of *R. maximum* seemed to be in the organic soil layer with increased amounts of low quality litter and humus with increased *R. maximum* basal area.

Our results, however, are correlative, which begs the question: does *R. maximum* influence forest floor properties or is the distribution of *R. maximum* determined by specific forest floor properties (acidic, low nutrient, large amounts of low quality litter and humus)? The distribution of *R. maximum* is generally in

low irradiance, moist areas (Lipscomb and Nilsen 1990), commonly coves and riparian areas in the southern Appalachians, although its distribution can follow moist slopes uphill. These coves can possess higher nutrient availability than the uphill slopes due to greater nitrogen mineralization (Knoepp and Swank 1998) and nutrient transfer downhill. While *R. maximum* is often found on low pH, low fertility sites, we feel that water availability is more important for determining *R. maximum* distribution than soil fertility or forest floor characteristics. *Rhododendron maximum* has very narrow xylem vessels (Lipp and Nilsen 1997) with low hydraulic conductivity, which will lead to high xylem tensions under high evaporative demand making it prone to summer drought-induced cavitation (Lipp and Nilsen 1997, Cordero and Nilsen 2002). This hydraulic limitation is likely more important in determining *R. maximum* distribution than soil fertility. Plants are easily grown in soils with relatively higher nutrient availability, as is done horticulturally. Additionally, the expansive range of *R. maximum* in the southern Appalachians crosses many soil series of varying nutrient availability. Thus, we feel that our findings support the conclusion that *R. maximum* is affecting forest floor properties, particularly in the organic layer.

Our study shows variation in forest floor and surface soil chemical properties along gradients of evergreen shrub basal area, particularly *R. maximum*. However, the trends differed somewhat at each site, so some of the variation in soil and forest floor properties observed in this study may have been due to site differences. The strength of the association between vegetation and forest floor and soil characteristics may be dependent upon the site forest management land-use history. Time since disturbance and the nature of the disturbance will influence the strength of the vegetation signal in the forest floor and soil resources. Forest floor resources are heterogeneous (Kleb and Wilson 1997), and that heterogeneity is highest early in forest development following disturbance (Guo et al. 2004). During succession to a mature stand, the factors that created the initial heterogeneity are reduced. In mature forest stands, soil resource heterogeneity is attributed to the legacy of initial heterogeneity and the individual influences of canopy trees and understory shrubs. For the most part, forest stands

in the Coweeta basin (LE and ME) have been unmanaged since around 1920 just prior to the establishment of the Nantahala National Forest. Therefore, forest floor and soil heterogeneity on our study sites may be a result of the early disturbance plus 80 to 100 years of vegetation influences. Over that time, the forest has undergone major changes such as a loss of *Castanea dentata* dominance, and an increase in understory shrub density. Our results indicate that understory evergreen shrubs may influence forest floor resource heterogeneity 100 years after disturbance in mature forest stands.

Moreover, different species of shrubs will have different effects on forest floor resource heterogeneity. The mosaic of subcanopy shrub distribution in a mature forest may be an important factor regulating the spatial variation of forest floor resources. There is ample documentation that evergreen, ericaceous shrubs inhibit tree regeneration in the southern Appalachian Mountains (Barden 1979, Phillips and Murdy 1985, Clinton et al. 1994, Beckage et al. 2000, Lei et al. 2002, Beckage and Clark 2003, Beckage et al. 2005, Beier et al. 2005). Many researchers have described the importance of these species from a population dynamics perspective (Bowers 1960; Day 1974; Hedman and Van Lear 1994; Dobbs 1995, 1998). Instead, we have attempted to demonstrate how these understory shrubs may regulate cycling of key elements through sequestration (Monk et al. 1985, Imm 1990) and transformation to recalcitrant forms in the associated forest floor. We have shown that these two important evergreen shrubs influence to varying degrees a variety of forest floor and soil properties. In general, there is greater accumulation of low quality litter and humus as well as a reduction of soil pH and some nutrients under *R. maximum* compared to areas with *K. latifolia* or to areas with no evergreen understory shrubs. The recalcitrant nature of these forest floor layers result in reduced quality, which may lead to lower nutrient levels in the forest floor and soil. This research is part of a larger study investigating the mechanisms by which evergreen ericaceous understory shrubs inhibit tree regeneration in the southern Appalachian mountains (Nilsen et al. 1999, Walker et al. 1999, Nilsen et al. 2001, Lei et al. 2002, Beier et al. 2005). Greater accumulation of low quality

litter and humus may contribute to the lack of successful recruitment of canopy tree seedlings underneath *R. maximum*.

The effects of *R. maximum*, and to a lesser extent *K. latifolia*, on tree recruitment are particularly relevant in light of the current losses of *Tsuga canadensis*, a common associate of *R. maximum*, as a result of woolly adelgid infestations (Ellison et al. 2005). On sites where *R. maximum* density is high, recruitment of *T. canadensis* or other species to replace lost overstory species is substantially diminished. The lack of recruitment has far-reaching consequences for future ecological structure and function in these areas.

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