

# Multifactor classification of forest landscape ecosystems of Jocassee Gorges, southern Appalachian Mountains, South Carolina

Scott R. Abella, Victor B. Shelburne, and Neil W. MacDonald

**Abstract:** Ecosystem classification identifies interrelationships within and among the geomorphology, soils, and vegetation that converge to form ecosystems across forest landscapes. We developed a multifactor ecosystem classification system for a 13 000 ha southern Appalachian landscape acquired in 1998 by the South Carolina Department of Natural Resources. Using a combination of multivariate analyses, we distinguished five ecosystem types ranging from xeric oak (*Quercus* spp.) to mesic eastern hemlock (*Tsuga canadensis* (L.) Carrière) ecosystems. Ecosystems segregated along geomorphic gradients influencing potential moisture availability, with soil properties such as solum thickness distinguishing among ecosystems occupying similar topographic positions. Our results suggest that different combinations of geomorphic and soil factors interact to form similar ecosystems across the landscape, and a given environmental factor can impact ecosystem development at some constituent sites of an ecosystem type but not at other sites. A regional comparison of ecosystem classifications indicates that environmental variables important for distinguishing ecosystems in the southern Appalachians vary, with Jocassee Gorges characterized by unique suites of environmental complexes. Our study supports the contention that the strengths of ecosystem classification are providing (i) comprehensive information on the interrelationships among ecosystem components, (ii) a foundation from which to develop ecologically based forest management plans, and (iii) an ecological framework in which to conduct future research on specific ecosystem components or processes.

**Résumé :** La classification des écosystèmes fait ressortir les interrelations dans et entre la géomorphologie, les sols et la végétation qui convergent pour former des écosystèmes dans les paysages forestiers. Nous avons mis au point un système multifactoriel de classification des écosystèmes pour une région de 13 000 ha dans la partie sud des Appalaches acquise en 1998 par le Département des ressources naturelles de la Caroline du Sud. À l'aide d'une combinaison d'analyses multivariées, nous avons distingué cinq types d'écosystèmes allant des écosystèmes xériques à chêne (*Quercus* spp.) aux écosystèmes mésiques à pruche du Canada (*Tsuga canadensis* (L.) Carrière). Les écosystèmes se sont regroupés le long de gradients géomorphologiques qui influencent la disponibilité potentielle en eau alors que les propriétés du sol telles que l'épaisseur du solum permettent de distinguer les écosystèmes qui occupent des positions topographiques similaires. Nos résultats indiquent que différentes combinaisons de facteurs géomorphologiques et pédologiques interagissent pour former des écosystèmes semblables dans le paysage et qu'un facteur environnemental donné peut influencer le développement de l'écosystème dans certains sites constitutifs d'un type d'écosystème mais pas dans d'autres sites. Une comparaison de la classification des écosystèmes à l'échelle régionale indique que les variables environnementales importantes pour distinguer les écosystèmes varient dans la partie sud des Appalaches telles que les Jocassee Gorges caractérisées par des ensembles uniques de complexes environnementaux. Notre étude supporte l'assertion que la solidité de la classification des écosystèmes procure (i) une information détaillée sur les interrelations entre les composantes de l'écosystème, (ii) les fondements sur lesquels on peut élaborer des plans d'aménagement forestier sur une base écologique et (iii) un cadre écologique pour conduire des recherches futures sur des composantes ou des processus spécifiques de l'écosystème.

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## Introduction

Landscape ecosystem classification is an integrative, multivariate approach for identifying interrelationships within and

among the vegetation, soils, and geomorphology of forest landscapes. The objectives of ecosystem classification are to identify patterns across the landscape, to distinguish reoccurring plant assemblages and their associated geomorphology

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and soils, and to describe the characteristics of the classified ecosystems to facilitate ecosystem identification (Whittaker 1962; Barnes et al. 1982; Host and Pregitzer 1992). An ecosystem classification incorporates the characteristics of inter-related sites, integrating information and facilitating communication about numerous sites of a landscape (Rowe and Sheard 1981; Pregitzer and Barnes 1984; Hix 1988).

Ecosystems segregate on a landscape along topographic and soil gradients impacting the distribution of vegetation (Spies and Barnes 1985; Archambault et al. 1990; McNab et al. 1999). In the Manistee National Forest of Michigan, for example, Host and Pregitzer (1992) found that glacial landforms, by influencing soil properties and disturbance regimes, constrained the distribution of ecosystems and their productivity. Mean annual biomass increment of overstory trees ranged from 1.3 t·ha<sup>-1</sup>·year<sup>-1</sup> in xeric oak (*Quercus* spp.) forests on sandy outwash plains to 3.6 t·ha<sup>-1</sup>·year<sup>-1</sup> in mesic sugar maple (*Acer saccharum* Marsh.) – red oak (*Quercus rubra* L.) forests on glacial moraines (Host et al. 1988). On the South Carolina Coastal Plain, Jones et al. (1984) distinguished ecosystems along a topographic gradient influencing the depth to groundwater, ranging from xeric uplands characterized by deep, sandy soils dominated by sparse overstories of turkey oak (*Quercus laevis* Walter) and longleaf pine (*Pinus palustris* Miller), to swamps consisting of bald-cypress (*Taxodium distichum* (L.) Rich.) and water tupelo (*Nyssa aquatica* L.). These examples from contrasting landscapes illustrate that the environmental factors influencing ecosystem distribution and the nature of ecosystem classification vary regionally, but the principle that an ecosystem results from a repeating combination of landforms, soils, and vegetation is consistent among landscapes (e.g., Mueller-Dombois 1964; Goebel et al. 2001).

The southern Appalachian landscape, not glaciated during the Pleistocene and containing the highest mountain ranges in the eastern United States, consists of a myriad of landforms of various sizes and shapes differing in moisture availability and impacting ecosystem distribution (Braun 1950; Callaway et al. 1987; McNab et al. 1999). While abrupt transitions do occur between ecosystems, much of the southern Appalachian landscape contains continua of subtle segregations of species varying with changes in topography (Day and Monk 1974). Ecosystem classification in the southern Appalachians must respond to high topographic diversity and complex topographic gradients in continuously varying forests (Whittaker 1967; Golden 1981).

This study was undertaken to develop a landscape ecosystem classification for Jocassee Gorges, a 13 000 ha contiguous Appalachian landscape acquired in 1998 by the South Carolina Department of Natural Resources. The South Carolina Department of Natural Resources is currently developing a forest management plan for Jocassee Gorges, but there is little existing published data for the area on which to base the plan. The objectives of this study were to (i) relate the distribution of late-successional vegetation to soils and landforms in an ecosystem classification system, (ii) elucidate reasons for the distribution of ecosystems across the landscape, and (iii) provide an ecological framework in which to develop a forest management plan and in which to conduct future research. This study focuses on landscape ecosystems occurring at scales of <1 to >10 ha and are anal-

ogous to the USDA Forest Service's landtype phases, the lowest classification level in the national hierarchical framework of ecological units of the United States (Cleland et al. 1997; Hix and Percy 1997; McMahan et al. 2001).

## Materials and methods

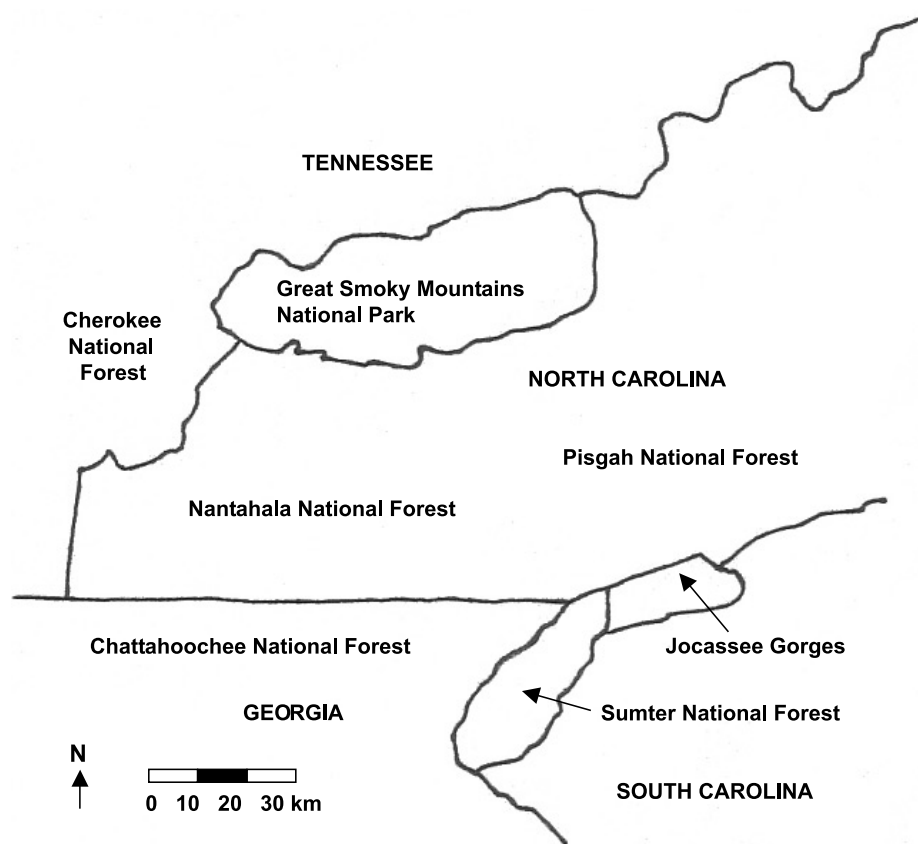
### Study area

Jocassee Gorges occurs in northern Oconee and Pickens counties in northwestern South Carolina along the South Carolina – North Carolina border (Fig. 1). Lying in the extreme southern section of the Blue Ridge Mountain physiographic province of the southern Appalachians, Jocassee Gorges occupies the southern chains of mountains that rise abruptly from the lower-elevation Piedmont region of South Carolina (Bowman 1911; Griffith et al. 2002). The topography of Jocassee Gorges consists of ridges, stream-dissected hillslopes composed of sideslopes and convex nose slopes between stream ravines, deep stream gorges, bottoms or steep slopes adjacent to large streams, and flat-floored coves embedded on upper slopes or near the origins of first-order streams. Slope gradients on hillslopes range from 20% to 70% and vary along the hillslope plan. Typical elevations in the study area range from 350 to 850 m, and elevations of the larger streams are 180–250 m lower than upper portions of surrounding hillslopes. Elevations of Jocassee Gorges are higher than those of the Piedmont region to the south but lower than the elevations of many mountain chains to the north in western North Carolina (Whittaker 1956; Carter et al. 2000). Within the study area, elevation does not impact ecosystem composition (Mowbray and Oosting 1968; Racine 1971) as it does in the higher-elevation mountains of the southern Appalachians (Callaway et al. 1987; McNab et al. 1999; Carter et al. 2000).

Major soil taxonomic categories in the study area include coarse-loamy, mixed, mesic Typic Dystrochrepts; fine-loamy, mixed, mesic Typic Hapludults; clayey, oxidic, mesic Typic Hapludults; fine-loamy, micaceous, thermic Typic Hapludults; and fine-loamy, mixed, mesic Humic Hapludults (Byrd 1963, 1972). Soils in the study area are typically shallow (solum thickness <70 cm), with A horizons <20 cm thick. Parent material of the soils includes granite, gneiss, or schist; as a result, soil is usually acidic (pH <6) throughout the profile.

Jocassee Gorges is in the extreme southern portion of the oak–chestnut forest region of Braun (1950). Presettlement vegetation was dominated by oaks and American chestnut (*Castanea dentata* (Marsh.) Borkh.) on hillslopes, which comprise the majority of the land area of the study area (Ayres and Ashe 1905; Holmes 1911; Braun 1950). Mountain laurel (*Kalmia latifolia* L.) and rhododendron (*Rhododendron* spp.) were characteristic shrubs of these oak–chestnut forests (Bartram 1791; Redfield 1879). Riparian vegetation consisted of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and a variety of hardwoods, often with understories of doghobble (*Leucothoe axillaris* var. *editorum* (Fernald and Schubert) Ahles) and rhododendron (Oosting and Billings 1939). Other common species in presettlement forests of the region included tulip-tree (*Liriodendron tulipifera* L.), hickories (*Carya* spp.), red maple (*Acer rubrum* L.), black-gum (*Nyssa sylvatica* Marsh.), Carolina

**Fig. 1.** Location of the 13 000 ha Jocassee Gorges (35°02'N, 82°50'W) in relation to the surrounding southern Appalachian landscape.



silverbell (*Halesia carolina* L.), sourwood (*Oxydendrum arboreum* (L.) DC.), and eastern flowering dogwood (*Cornus florida* L.).

#### Stand selection and plot location

We digitized locations of the >350 stands in the study area from stand maps provided by Crescent Resources, Inc., a land and timber company that managed Jocassee Gorges until the area was acquired in 1998 by the South Carolina Department of Natural Resources. Using these stand records combined with field reconnaissance, we identified areas to be sampled in 48 stands distributed across the landscape that had no known history of major disturbance in at least the past 70 years. Previous research has demonstrated that geomorphology is a primary factor controlling the distribution of vegetation in the Appalachian Mountains (Braun 1950; Whittaker 1956; Hack and Goodlett 1960), and based on this previous research, we randomly selected in each of the 48 stands one of eight topographic positions to be sampled. Topographic positions included stream bottoms, ridgetops, and lower, middle, and upper slope positions on both north-facing (270–90°) and south-facing (90–270°) slopes. If topographic maps and field reconnaissance indicated that the randomly selected topographic position did not occur in the stand or did not meet our disturbance criteria, we randomly selected another topographic position to be sampled in that stand. We randomly located one 0.1-ha, 20 m × 50 m plot (dimensions were corrected for slope gradient to be 0.1 ha on a horizontal plane; Husch et al. 1982) oriented parallel to

contours within the assigned topographic position of each of the 48 stands for a total of 48 plots. Plots represented independent sampling units across the landscape (Hurlbert 1984). Because we did not locate plots within a priori defined ecosystems, a common procedure in ecosystem classification research, our sampling design and independence of plots facilitated our sampling of the full forest continuum.

#### Plot sampling

In each plot, we sampled geomorphology, soils, and vegetation; sampling occurred from 1 May to 26 September 2001. At plot centers, we determined aspect, slope gradient, landform index (McNab 1993), and terrain shape index (McNab 1989). Landform index quantifies site protection by landforms surrounding a plot, with high values of the index (e.g., 40) occurring in coves and stream ravines where protection is high and low values (e.g., 10) occurring on exposed sites such as ridgetops (McNab 1993). Terrain shape index, a measure of land surface curvature at the plot scale, was determined from the plot center to land surfaces surrounding a plot at a distance of 20 m from the plot center (McNab 1989). Average measurement error ( $(|original\ measure - repeated\ measure| / original\ measure) \times 100$ ), based on one repeated measure for each of 10 randomly selected plots, was  $4.3 \pm 1.7\%$  (mean  $\pm$  95% confidence interval) for landform index,  $58.4 \pm 62.7\%$  for terrain shape index, and  $2.1 \pm 1.0\%$  for slope gradient. Although measurement errors have not previously been published for terrain shape index, our results suggest the index is difficult to measure

reproducibly; therefore, we did not use the index in statistical analyses. Plot surface shape (convex, concave, or linear) was described downslope and across the slope (Wilson 1968; Ruhe 1975).

We determined species and measured diameter to the nearest 0.1 cm for all live trees >1 cm in diameter in the 0.1-ha plots. Species were classified as trees for these measurements following Radford et al. (1968); nontree species were inventoried as ground-flora. We divided plots into ten 10 m × 10 m (0.01 ha) subplots to inventory ground-flora (vascular plants including tree seedlings and saplings <1 cm in diameter at 1.37 m) rooted in subplots by species. Each subplot was traversed until no new species were found, and the areal percent cover of each species was visually categorized for each subplot using 10 cover classes in Peet et al. (1998). Plant nomenclature follows Radford et al. (1968).

We sampled soils on each plot using a bucket auger in the centers of two randomly selected subplots (Soil Survey Division Staff 1993). We measured the thickness of the Oe + Oa horizon to the nearest 0.5 cm in four cardinal directions 2 m from each soil sampling location. All horizon thickness measurements were averaged on a plot basis. We composited soil in the field throughout each horizon for the A and B horizons, and we composited samples from both subplots into one plot sample each for the A and B horizons for laboratory analysis (48 plots × 2 horizons per plot = 96 total composite samples).

#### Soil laboratory analysis

We determined moist soil color for each soil sample under outdoor lighting using Munsell color charts. Based on one repeated color determination for each of 10 randomly selected samples, seven samples exhibited repeated determinations identical to original determinations and three samples differed by one unit of value or chroma. After sieving the samples through a 2-mm sieve, we analyzed the samples for texture (hydrometer method), organic C (Walkley-Black procedure of H<sub>2</sub>SO<sub>4</sub>-K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub> oxidation followed by titration with FeSO<sub>4</sub>), and pH (1:1 soil-water) following methods in Klute (1986) and Page et al. (1982). Average measurement error, based on one repeated measure for each of the A and B horizon samples for six randomly selected plots, was 1.6 ± 0.6% (mean ± 95% confidence interval) for sand, 3.4 ± 1.5% for silt, 2.2 ± 1.2% for clay, 4.6 ± 2.2% for organic C, and 0.3 ± 0.1% for pH.

#### Data summary

Slope aspect was transformed following Beers et al. (1966). Categorical variables (landform shape (convex, linear, or concave), plot surface shape (combinations of across-slope and down-slope shapes), landform type (ridgetop, hillslope, cove, stream ravine, or stream bottom), broad landform aspect (90–270° or 270–90°), and slope position (upper, middle, or lower)) were ranked according to potential moisture availability. We integrated geomorphic characteristics for each plot using the topographic relative moisture index (ranges from 0 on xeric sites to 100 on mesic sites) expressed as a percentage by scaling measurements of aspect, slope position, slope shape, and slope gradient following Parker (1982). We calculated importance values for trees (average of relative density and relative basal area) and

ground-flora (average of relative cover class and relative frequency (based on 10 subplots per plot)) for each species on each plot.

#### Statistical analyses

We developed the ecosystem classification by ordinating and classifying the 28 environmental variables measured in this study using principal components analysis (PCA) (cross-products matrix derived from correlation coefficients) and cluster analysis (Ward's group linkage method, variables rank transformed) and the vegetation and environment combined using canonical correspondence analysis (CCA) (plot scores derived from species). We used species importance values for the vegetation analyses, and species occurring in less than three plots were removed from the data set before analysis (Gauch 1982). All analyses were conducted using the software PC-ORD (McCune and Mefford 1999). Classification and ordination techniques both identified similar plot groupings, strengthening the robustness of the classification. This ecosystem classification represents an inclusive multifactor approach integrating and providing equal weight to the three ecosystem components of geomorphology, soils, and vegetation in a corroborative suite of multivariate analyses.

We compared overall vegetation and environmental composition among the classified ecosystems using pairwise multiresponse permutation procedure (MRPP) tests in PC-ORD (McCune and Mefford 1999). MRPPs are multivariate, nonparametric tests that evaluate the null hypothesis of no difference in composition between groups using a randomization procedure. A significant result indicates that clustering within groups is greater than expected by chance (McCune and Mefford 1999). This analysis, therefore, provides a means for assessing the distinctness of each ecosystem in vegetation and environmental composition. Environmental variables were rank transformed before this analysis to provide equal weighting to each variable. Using the six most important environmental variables identified by CCA, we tested the null hypothesis of no relationship of these variables with the vegetation matrix using the Monte Carlo test associated with CCA (McCune and Mefford 1999). We also conducted univariate tests of mean soil and topographic variables among the ecosystems using one-way analyses of variance and Tukey's multiple comparison test (SAS Institute Inc. 1999). Data not meeting the assumptions of homogeneity of variance or normality were logarithmic or arcsine transformed before analysis (SAS Institute Inc. 1999).

## Results and discussion

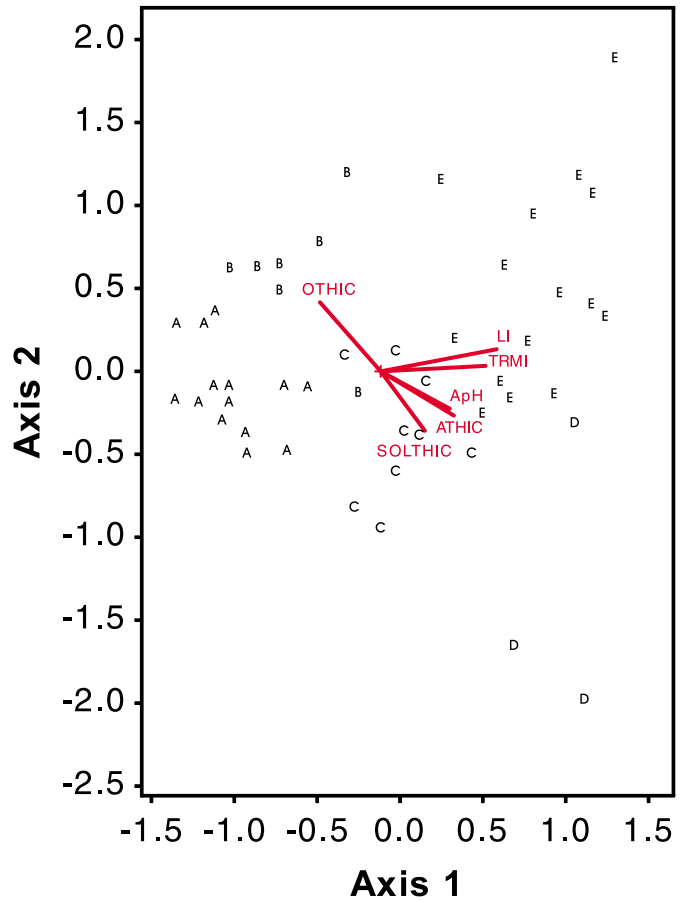
### Classification

Five ecosystem types were distinguished and named according to their inferred moisture status, dominant overstory species, and characteristic ground-flora composition: xeric oak-blueberry, xeric chestnut oak – mountain laurel, sub-mesic oak – mixed flora, mesic hardwoods-bloodroot, and mesic hemlock-rhododendron (Table 1). These ecosystems represented repeating combinations across the landscape of landforms, soils, and their associated plant assemblages. Cluster analysis combined with ordination results indicate

**Table 1.** Summary of ecosystem characteristics for forest ecosystems of Jocassee Gorges, southern Appalachian Mountains.

Ecosystem type	
Characteristic	
Overstory dominants*	Xeric oak–blueberry <i>Quercus coccinea</i> (11), <i>Quercus velutina</i> (6)
Understory dominants	Xeric chestnut oak – mountain laurel <i>Quercus prinus</i> (33) <i>Oxydendrum arboreum</i> (9), <i>Nyssa sylvatica</i> (5), <i>Acer rubrum</i> (23)
Ground-flora dominants	Submesic oak – mixed flora <i>Quercus alba</i> (13), <i>Carya</i> spp. (9) <i>Halesia carolina</i> (4), <i>Magnolia fraseri</i> (4)
Topography	Mesic hardwoods–bloodroot <i>Liriodendron tulipifera</i> (35) <i>Halesia carolina</i> (10) <i>Sanguinaria canadensis</i> (2), <i>Adiantum pedatum</i> (1)
Typical aspects (°)	Mesic hemlock–rhododendron <i>Tsuga canadensis</i> (34), <i>Liriodendron tulipifera</i> (11) <i>Betula lenta</i> (6), <i>Fagus grandifolia</i> (4)
Typical soils	Mesic hemlock–rhododendron <i>Leucothoe axillaris</i> (4) Stream bottoms, stream ravines, lower slopes All aspects Variable
	Mesic hardwoods–bloodroot Concave landforms, coves, lower slopes 315–60 Sola >100 cm thick, A horizon chroma <2
	Submesic oak – mixed flora Coves, stream ravines All aspects Variable
	Xeric chestnut oak – mountain laurel Upper slopes 270–90 Coarse textured, rocky slopes
	Xeric oak–blueberry Ridgetops, convex nose slopes, upper slopes 90–270 High B horizon clay

\*Mean importance values (%) in an ecosystem type follow the species name (tree importance values are the average of relative density and relative basal area; ground-flora importance values are the average of relative cover class and relative frequency). Importance values were computed separately for the overall tree and ground-flora matrices.



**Fig. 2.** Canonical correspondence analysis ordination of forest ecosystems of Jocassee Gorges, southern Appalachian Mountains. Ecosystems: A, xeric oak–blueberry; B, xeric chestnut oak – mountain laurel; C, submesic oak – mixed flora; D, mesic hardwoods–bloodroot; E, mesic hemlock–rhododendron. Environmental variables: ApH, A horizon pH; ATHIC, A horizon thickness; LI, landform index; OTHIC, Oe + Oa horizon thickness; SOLTHIC, solum thickness; TRMI, topographic relative moisture index.

that the vegetation consistently expressed environmental conditions (Fig. 2).

Ordination reflected the continuous variability of forest environmental and vegetation complexes (Fig. 2), and a criticism of ecosystem classification is that classification imposes artificial divisions on systems that vary continuously (sensu Kent et al. 1997). However, MRPP tests indicated that several ecosystems differed significantly in environmental composition, and all ecosystems differed in vegetation composition (Table 2). These results demonstrate that similar sites do reoccur on forest landscapes, and collections of forest sites representing an ecosystem are statistically different in composition from constituent sites of other ecosystem types. The data suggest that the ecosystem types are natural ecological units of the landscape characterized by specific ranges of ecological properties, and the ecosystem classification was effective for summarizing the range of variability of forest sites on this landscape.

Geomorphic complexes differed significantly between xeric and mesic ecosystems (Table 2). However, geomorphic

**Table 2.** Multiresponse permutation procedure tests of environmental and vegetation matrices among forest ecosystems of Jocassee Gorges, southern Appalachian Mountains.

Matrix	Mean Euclidean distance* for ecosystem type <sup>†</sup>					$T^{\ddagger}$	$P$	Delta <sup>§</sup>	$A^{\parallel}$
	X O/B	X C/ML	S O/MF	M H/B	M H/R				
Soils	68a	71b	69c	51d	84bc	-7.39	<0.0001	72.9	0.09
Geomorphology	34a	45b	48c	49c	51c	-11.27	<0.0001	44.6	0.21
Environment <sup>¶</sup>	78a	86b	85c	71d	99c	-11.21	<0.0001	86.6	0.13
Vegetation	35a	29b	32c	34d	36e	-17.65	<0.0001	33.8	0.27
Understory only**	29a	30b	40c	46c	38d	-13.27	<0.0001	35.1	0.31

**Note:** Letters summarize pairwise comparisons, and ecosystems within a row without shared letters differ at  $P < 0.05$ .

\*Higher distances indicate greater heterogeneity within an ecosystem type.

<sup>†</sup>X O/B, xeric oak–blueberry; X C/ML, xeric chestnut oak – mountain laurel; S O/MF, submesic oak – mixed flora; M H/B, mesic hardwoods–bloodroot; M H/R, mesic hemlock–rhododendron.

<sup>‡</sup> $T$  statistic and probability associated with overall multiresponse permutation procedure test for each matrix.

<sup>§</sup>Delta is the weighted mean within-group distance.

<sup>¶</sup>A statistic (chance-corrected within-group agreement).

<sup>\*\*</sup>Soil (18 variables) and geomorphology (10 variables) matrices combined.

<sup>\*\*</sup>Matrix of relative densities of trees 1–10 cm in diameter.

complexes did not differ among the three mesic ecosystems, reflecting the similarity and variety of topographic positions on which these ecosystems occur and the need to include soil variables to distinguish these ecosystems. The mesic hardwoods–bloodroot ecosystem exhibited a distinct combination of soil properties (thick sola, thin Oe + Oa horizons, higher soil pH), separating this ecosystem from other mesic ecosystems. The submesic oak – mixed flora and mesic hemlock–rhododendron ecosystems were the only ecosystems that did not differ from each other in overall environmental composition. Geomorphic and soil complexes were extremely variable in the mesic hemlock–rhododendron ecosystem, making it difficult to detect differences (Table 2). In contrast with vegetation where all vascular plant species were measured, the 28 environmental variables measured in this study are only a fraction of the total that could be measured (Billings 1952). It is possible that soil nutrients or hydrological variables not measured in this study could have distinguished the submesic oak – mixed flora and mesic hemlock–rhododendron ecosystems. Additional research examining soil nutrient or hydrological variables not measured in this study could be undertaken to refine differences in environmental complexes among the ecosystems.

Ecosystem classification has been criticized for not being responsive to temporal transitions in vegetation due to the occurrence or absence of disturbance (Ecological Society of America Vegetation Classification Panel 2002). For example, three of the ecosystems in this study are dominated by oaks, but given the current lack of disturbance in the southern Appalachians, it seems unlikely that oak dominance will persist (Lorimer 1993; Brose et al. 2001). However, 9 of 10 MRPP pairwise comparisons of understory composition (1–10 cm in diameter) between ecosystems were significant (Table 2). Understory composition provides a measure of possible future forest composition (Oliver and Larson 1996), and although understories of the oak ecosystems were dominated by species other than oaks (e.g., black-gum, red maple, tulip-tree), the ecosystem types still supported distinct understory assemblages and remained in their ecosystem groupings (Table 2). These data suggest that vegetation changes in the ecosystems are constrained by underlying

environmental influences, and the ecosystem classification will remain viable, although with different vegetative composition, during the future period of reduced fire frequencies expected to characterize many areas of the southern Appalachians (Brose et al. 2001).

## Ecosystem components

### Vegetation

Oaks (*Quercus coccinea* Muenchh., *Quercus velutina* Lam., *Quercus alba* L., and *Quercus prinus* L.) dominated much of the landscape (Table 3), consistent with the inclusion of the study area in the oak–chestnut forest region (Braun 1950). The null hypothesis of the CCA Monte Carlo test of no relationship between vegetation and environmental matrices was rejected (axis 1 eigenvalue = 0.34,  $P < 0.001$ ; axis 2 eigenvalue = 0.10,  $P < 0.001$ ). Variables exhibiting the highest correlations (interset correlations because WA scores were used; ter Braak 1986) with axis 1 were landform index (-0.83) and the topographic relative moisture index (-0.76), and for axis 2 Oe + Oa horizon thickness (0.61) and solum thickness (-0.52).

### Geomorphology and soils

Ecosystems differentiated along geomorphic gradients influencing potential moisture availability, consistent with ecosystem classifications in other regions (e.g., Jones et al. 1984; Host and Pregitzer 1992; Hix and Percy 1997). Landform index and the topographic relative moisture index were higher in mesic ecosystems than in xeric ecosystems (Table 4), indicating that topography at both broad and fine scales impacted ecosystem distribution. For example, ecosystems occurring along streams flowing down hillslopes became more mesic as the streams descended to lower slope positions, where topographic protection (indicated by high landform indices) and moisture accumulation are greater (Hack and Goodlett 1960; Helvey et al. 1972). These results suggest that ecosystem classification in the southern Appalachians is most accurate when both the local topographic form and the position of the topographic feature on the landscape are examined simultaneously.

**Table 3.** Mean basal area ( $\text{m}^2\text{-ha}^{-1}$ ) and density ( $\text{trees}\cdot\text{ha}^{-1}$ ) for live trees  $>1$  cm in diameter by ecosystem type for forest ecosystems of Jocassee Gorges, southern Appalachian Mountains.

Species <sup>†</sup>	Measure <sup>‡</sup>	Ecosystem type*									
		X O/B		X C/ML		S O/MF		M H/B		M H/R	
		Mean <sup>§</sup>	CV <sup>  </sup>	Mean	CV	Mean	CV	Mean	CV	Mean	CV
<i>Acer rubrum</i>	BA	4.8	53	6.2	52	4.0	58	4.1	73	3.4	101
	D	479	32	459	32	353	41	230	53	165	81
<i>Betula lenta</i>	BA	Tr	374	0.1	207	0.2	251	1.0	150	2.4	106
	D	2	374	12	230	14	139	17	69	73	89
<i>Carya</i> spp.	BA	2.3	123	3.0	121	4.9	55	2.5	153	2.9	147
	D	72	138	51	64	69	54	130	122	59	101
<i>Cornus florida</i>	BA	0.3	97	0.4	74	0.4	97	0.2	114	0.1	117
	D	94	75	111	68	102	68	53	103	31	128
<i>Fagus grandifolia</i>	BA	Tr	306	Tr	172	0.3	278	0.4	173	1.5	155
	D	3	289	4	184	26	178	80	173	61	77
<i>Halesia carolina</i>	BA	Tr	374	Tr	265	0.2	139	1.4	104	0.1	320
	D	1	374	13	265	98	121	170	51	17	204
<i>Liriodendron tulipifera</i>	BA	1.3	210	1.1	107	4.9	84	27.4	70	6.9	41
	D	55	132	36	120	121	119	113	89	56	52
<i>Magnolia acuminata</i>	BA	0.2	355	Tr	265	0.1	140	0.1	173	0.5	174
	D	2	199	1	265	11	177	10	173	8	165
<i>Magnolia fraseri</i>	BA	Tr	281	Tr	259	0.2	106	Tr	101	0.5	181
	D	16	134	5	191	118	135	27	43	19	99
<i>Nyssa sylvatica</i>	BA	2.7	59	0.8	184	0.4	132	Tr	173	0.2	214
	D	344	52	116	83	58	83	10	173	15	161
<i>Oxydendrum arboreum</i>	BA	2.5	39	2.3	43	1.5	92	Tr	173	0.7	100
	D	205	52	177	34	128	65	3	173	37	108
<i>Pinus strobus</i>	BA	0.3	173	—	—	0.3	190	—	—	2.5	162
	D	25	165	—	—	30	146	—	—	34	176
<i>Pinus</i> spp.	BA	0.9	183	0.4	173	0.1	300	—	—	0.1	387
	D	25	197	3	171	1	300	—	—	1	387
<i>Quercus alba</i>	BA	5.1	92	—	—	7.9	78	—	—	2.7	113
	D	67	79	—	—	56	85	—	—	19	126
<i>Quercus prinus</i>	BA	4.5	128	21.5	44	5.7	105	—	—	1.5	233
	D	86	130	230	45	50	107	—	—	14	196
<i>Quercus</i> spp.	BA	9.5	53	2.5	106	5.4	88	Tr	173	1.2	137
	D	114	61	33	104	22	77	3	173	11	109
<i>Robinia pseudo-acacia</i>	BA	0.8	196	2.0	93	0.8	228	1.9	173	0.7	192
	D	8	114	26	101	4	119	7	173	9	174
<i>Tilia americana</i>	BA	—	—	—	—	0.4	299	1.8	158	1.4	164
	D	—	—	—	—	7	212	100	87	31	152
<i>Tsuga canadensis</i>	BA	Tr	160	0.2	177	0.7	132	1.1	131	10.2	70
	D	9	188	41	187	111	143	133	120	619	59
Other spp.	BA	Tr	163	Tr	149	Tr	136	0.2	172	Tr	346
	D	10	130	6	138	16	164	23	138	5	179
Other mesic spp.	BA	—	—	Tr	173	0.5	203	0.1	124	0.5	134
	D	—	—	8	172	24	128	93	115	44	112
Total	BA	35.2	21	40.4	14	39.0	22	42.1	30	40.0	19
	D	1619	23	1334	21	1419	27	1203	53	1327	42

\*X O/B, xeric oak–blueberry; X C/ML, xeric chestnut oak – mountain laurel; S O/MF, submesic oak – mixed flora; M H/B, mesic hardwoods–bloodroot; M H/R, mesic hemlock–rhododendron.

<sup>†</sup>*Carya* spp. includes *C. tomentosa*, *C. glabra*, and *C. pallida*; *Pinus* spp. includes *P. rigida*, *P. echinata*, and *P. virginiana*; *Quercus* spp. includes *Q. coccinea*, *Q. velutina*, and *Q. rubra*; other spp. includes *Castanea dentata*, *Ilex opaca*, *Sassafras albidum*, *Amelanchier arborea*, and *Prunus serotina*; other mesic spp. includes *Liquidambar styraciflua*, *Hamamelis virginiana*, *Cornus alternifolia*, *Fraxinus americana*, and *Carpinus caroliniana*.

<sup>‡</sup>BA, basal area; D, density.

<sup>§</sup>Tr, trace (rounds to zero); —, species not present.

<sup>||</sup>Coefficient of variation (%).

**Table 4.** Means and ranges of topographic variables by ecosystem type for forest ecosystems of Jocassee Gorges, southern Appalachian Mountains.

Variable	Ecosystem type*					$F^{\dagger}$	$P$
	X O/B	X C/ML	S O/MF	M H/B	M H/R		
Landform index <sup>‡</sup>							
Mean <sup>§</sup>	16c (47)	23bc (19)	29ab (17)	35a (16)	34a (21)	17.01	<0.0001
Range	1–25	18–28	23–37	31–41	24–53		
TRMI <sup>  </sup>							
Mean	29c (43)	40bc (27)	51ab (21)	65a (5)	60a (26)	13.15	<0.0001
Range	13–55	28–55	35–65	62–68	42–90		
Slope gradient (%)							
Mean	38 (39)	60 (13)	49 (34)	36 (45)	53 (64)	1.49	0.2210
Range	2–57	52–75	19–70	19–51	2–94		
Transformed aspect <sup>¶</sup>							
Mean	0.83 (48)	1.22 (71)	1.16 (69)	1.21 (68)	1.08 (50)	0.67	0.6142
Range	0.28–1.62	0.05–2.00	0.00–2.00	0.36–1.99	0.26–2.00		

**Note:** Means within a row without shared letters differ at  $P < 0.05$ .

\*X O/B, xeric oak–blueberry; X C/ML, xeric chestnut oak – mountain laurel; S O/MF, submesic oak – mixed flora; M H/B, mesic hardwoods–bloodroot; M H/R, mesic hemlock–rhododendron.

<sup>†</sup> $F$  statistic and probability associated with a one-way analysis of variance.

<sup>‡</sup>Landform index is a measure of site exposure with increasing values indicating increasing protection from solar radiation by the surrounding topography (McNab 1993).

<sup>§</sup>Values are means (coefficient of variation (%)).

<sup>||</sup>Topographic relative moisture index (ranges from 0 on xeric sites to 100 on mesic sites).

<sup>¶</sup>Ranges from 0 (225°) to 2 (45°).

Soil properties contributed to the specificity of the ecosystems and were important for distinguishing several ecosystems (Table 5). Mean sand and clay concentrations in the B horizon differed between the xeric ecosystems, with higher clay and lower sand occurring in the oak–blueberry ecosystem than in the chestnut oak – mountain laurel ecosystem. Higher B horizon clay in the oak–blueberry ecosystem reflects this ecosystem's frequent occurrence on south-facing upper slopes where weathering is intense (Graham et al. 1990; Graham and Buol 1990). These results are consistent with studies in areas adjacent to Jocassee Gorges (Mowbray and Oosting 1968; Losche et al. 1970) but for reasons that remain unclear differ from those of Daniels et al. (1987a, 1987b), who found higher clay concentrations on north-facing than on south-facing slopes in the Joyce Kilmer Memorial Forest in western North Carolina. Higher B horizon sand concentrations in the chestnut oak – mountain laurel ecosystem than in the oak–blueberry ecosystem result from lower weathering on north aspects where the chestnut oak ecosystem often occurs and from the tendency of this ecosystem to occur on slopes characterized by boulders and rock outcrops that generate coarse fragments when weathered (Daniels et al. 1987a). Dominance of chestnut oak on rocky slopes is consistent with the published silvics of this species (Burns and Honkala 1990). Soil properties partially distinguish the two xeric ecosystems from each other on sites where geomorphology is similar between the ecosystems.

The mesic hardwoods–bloodroot ecosystem occupied topographic positions typically supporting the mesic hemlock–rhododendron or the submesic oak – mixed flora ecosystems, but this ecosystem was differentiated by higher soil pH combined with A horizons and sola twice as thick as in the other ecosystems (Table 5). These soils had large soil volumes favorable for root penetration (Stone and Kalisz 1991;

Richter and Markewitz 1995), high total organic matter content, and a large water-holding capacity when combined with elevated levels of A horizon silt (Yeakley et al. 1998). Higher pH values in the hardwoods–bloodroot ecosystem, combined with the absence of heavy shade from hemlock and ericaceous shrubs (Daubenmire 1929; Oosting and Billings 1939), contributed to the rich layer of such forest herbs as ginseng (*Panax quinquefolium* L.) and blue cohosh (*Caulophyllum thalictroides* (L.) Michaux) common in the hardwoods–bloodroot ecosystem but rare elsewhere (Graves and Monk 1985).

Mean Oe + Oa horizon thickness was low in the mesic ecosystems compared with the xeric ecosystems, consistent with an ecosystem classification study in an area adjacent to Jocassee Gorges (Hutto et al. 1999). The hardwoods–bloodroot ecosystem exhibited the thinnest Oe + Oa horizons, reflecting a high decomposition rate and the absence in this ecosystem of hemlock and ericaceous litter resistant to decomposition. In contrast, the chestnut oak – mountain laurel ecosystem exhibited thick Oe + Oa horizons because of slow decomposition on the xeric sites that the ecosystem frequently occupied, in combination with litter derived from chestnut oak and mountain laurel resistant to decomposition (Mudrick et al. 1994). These examples illustrate that the current soils of the ecosystems partly reflect long-term interactions with vegetation.

Several soil properties, when used in combination, are useful for identifying the ecosystems in the field (Table 5). For example, thickness of the Oe + Oa horizon can be determined rapidly and, when combined with soil color, can be used to distinguish the hardwoods–bloodroot ecosystem from other ecosystems. Our results additionally show that despite a general uniformity of texture and solum thickness across the landscape (Table 5), as was also documented in previous studies in the southern Appalachians (Neary et al.

**Table 5.** Means and ranges of soil variables for forest ecosystems of Jocassee Gorges, southern Appalachian Mountains.

Variable	Measure	Ecosystem type*					<i>F</i> <sup>†</sup>	<i>P</i>
		X O/B	X C/ML	S O/MF	M H/B	M H/R		
A horizon texture (%)								
Sand	Mean <sup>‡</sup>	59 (8)	63 (4)	61 (6)	56 (7)	59 (16)	1.08	0.378
	Range	51–67	60–68	57–69	51–58	39–76		
Silt	Mean	26 (14)	25 (10)	27 (12)	34 (4)	28 (22)	2.55	0.053
	Range	20–34	21–28	22–31	32–35	14–39		
Clay	Mean	15 (19)	12 (19)	12 (18)	11 (21)	13 (39)	1.78	0.151
	Range	11–21	8–15	8–16	9–14	7–24		
B horizon texture (%)								
Sand	Mean	52b (11)	63a (8)	60ab (9)	60ab (7)	60ab (21)	2.81	0.037
	Range	42–61	55–69	48–67	57–65	37–82		
Silt	Mean	23 (24)	21 (13)	22 (13)	23 (5)	23 (29)	0.39	0.812
	Range	17–36	17–25	18–28	22–25	7–32		
Clay	Mean	25a (34)	16b (23)	18ab (34)	17ab (33)	16ab (58)	3.03	0.027
	Range	13–41	12–23	13–34	10–20	9–44		
Organic carbon (%)								
A horizon	Mean	3.3 (38)	3.3 (29)	3.7 (25)	5.2 (29)	3.7 (32)	1.82	0.142
	Range	1.3–5.4	1.9–4.5	2.3–5.3	3.6–6.6	2.4–6.8		
B horizon	Mean	0.7 (73)	0.8 (56)	0.8 (78)	0.8 (15)	1.2 (73)	1.49	0.221
	Range	0.3–2.4	0.5–1.7	0.3–2.2	0.6–0.8	0.5–3.8		
pH								
A horizon	Mean	4.53b (3)	4.66b (5)	4.85ab (4)	5.05a (0)	4.82ab (6)	6.23	<0.001
	Range	4.25–4.77	4.37–4.99	4.62–5.26	5.04–5.07	4.25–5.37		
B horizon	Mean	4.80 (3)	4.84 (4)	4.95 (3)	5.07 (3)	4.90 (3)	2.47	0.059
	Range	4.55–5.01	4.64–5.11	4.71–5.20	4.96–5.21	4.61–5.22		
Color (Munsell units) <sup>§</sup>								
A horizon value	Mean	3.7a (16)	3.9a (10)	3.2ab (14)	2.8b (10)	3.3ab (14)	4.65	0.003
	Range	3–5	3–4	3–4	2–3	3–4		
A horizon chroma	Mean	3.9a (34)	3.3ab (23)	2.3bc (21)	1.7c (35)	2.3bc (31)	12.1	<0.001
	Range	3–8	2–4	2–3	1–2	2–6		
B horizon value	Mean	4.6 (17)	4.4 (12)	4.2 (10)	4.0 (25)	4.1 (15)	1.16	0.342
	Range	4–6	4–5	4–5	3–5	3–5		
B horizon chroma	Mean	6.3a (17)	6.3a (29)	5.1ab (21)	3.3b (17)	5.3ab (37)	3.24	0.021
	Range	4–8	4–8	4–6	3–4	2–8		
Thickness (cm)								
Oe + Oa horizon	Mean	3.0ab (19)	3.7a (37)	1.9c (21)	0.8d (75)	2.3bc (49)	9.73	<0.001
	Range	2.2–4.1	1.4–5.1	1.5–2.8	0.1–1.1	0.8–4.1		
A horizon	Mean	12b (30)	14b (30)	17b (32)	30a (37)	17b (34)	6.51	<0.001
	Range	7–22	9–21	12–29	19–41	9–33		
Solum	Mean	59b (16)	58b (16)	63b (22)	120a (19)	62b (31)	6.75	<0.001
	Range	41–71	47–71	45–90	98–143	36–98		

**Note:** Means within a row without shared letters differ at  $P < 0.05$ .

\*X O/B, xeric oak–blueberry; X C/ML, xeric chestnut oak – mountain laurel; S O/MF, submesic oak – mixed flora; M H/B, mesic hardwoods–bloodroot; M H/R, mesic hemlock–rhododendron.

<sup>†</sup>*F* statistic and probability associated with a one-way analysis of variance.

<sup>‡</sup>Values are means (coefficient of variation (%)).

<sup>§</sup>Hues were in the ranges 2.5–10YR and 2.5–5Y.

1986; Daniels et al. 1987a), soil properties are key secondary factors distinguishing ecosystems occupying similar topographic positions in the southern Appalachians.

### Interrelationships

Separate PCAs of the soil, geomorphic, and combined 28-variable environmental matrices indicated that the first three principal components (PC) explained between 53% (combined matrix) and 78% (geomorphic matrix) of the variance of the data sets (Table 6). In the soils PCA, the first PC rep-

resents a pH, color, and B horizon texture gradient, the second PC a horizon thickness and A horizon texture gradient, and the third PC an organic C gradient. Eleven of 18 soil variables exhibited loadings of 0.3 or higher on at least one PC. Six of the 10 geomorphic variables exhibited loadings greater than 0.3 on the first PC of the geomorphic PCA, and all variables exhibited loadings higher than 0.3 on one or more PCs. The first PC is a landform shape and topographic protection gradient, the second PC an aspect gradient, and the third PC a gradient in percent slope. No variables exhib-

**Table 6.** Summary of separate principal components analyses for soil, geomorphic, and combined soil and geomorphic matrices for forest ecosystems of Jocassee Gorges, southern Appalachian Mountains.

Variable	PC1	PC2	PC3
<b>Soil PCA</b>			
A horizon sand	0.22	0.38	-0.19
A horizon silt	-0.06	-0.37	0.16
A horizon clay	-0.30	-0.19	0.12
A horizon pH	0.29	-0.14	-0.20
A horizon organic C	0.10	-0.18	0.43
A horizon value	-0.27	0.16	-0.20
A horizon chroma	-0.33	0.08	-0.24
A horizon thickness	0.27	-0.14	-0.15
B horizon sand	0.32	0.27	0.01
B horizon silt	-0.15	-0.20	0.24
B horizon clay	-0.26	-0.17	-0.15
B horizon pH	0.28	-0.14	-0.33
B horizon organic C	0.09	0.08	0.49
B horizon value	-0.24	0.09	-0.11
B horizon chroma	-0.34	0.05	-0.21
B horizon thickness	-0.01	-0.41	-0.17
Oe + Oa horizon thickness	-0.22	0.26	0.16
Solum thickness	0.08	-0.40	-0.20
Eigenvalue	4.79	4.03	2.46
Broken-stick eigenvalue	3.50	2.50	2.00
% variance explained	6.6	22.4	13.7
<b>Geomorphic PCA</b>			
First- to third-order stream	-0.23	0.37	0.32
Landform shape	-0.40	0.17	-0.01
Landform type	-0.41	0.22	-0.10
Landform index	-0.37	0.06	0.30
Plot surface shape	-0.38	-0.10	-0.29
Slope gradient	-0.02	0.05	0.77
Hillslope aspect	-0.16	-0.56	0.11
Slope position	-0.36	0.07	-0.04
Transformed plot aspect	-0.09	-0.61	0.28
TRMI*	-0.41	-0.28	-0.19
Eigenvalue	4.60	1.76	1.47
Broken-stick eigenvalue	2.93	1.93	1.43
% variance explained	46.0	17.6	14.7
<b>Combined PCA</b>			
Landform index	-0.29	0.03	-0.12
TRMI*	-0.28	0.08	-0.13
Landform shape	-0.28	0.01	0.09
Plot surface shape	-0.27	0.01	-0.01
Landform type	-0.28	-0.04	0.07
Slope position	-0.24	0.06	-0.01
Solum thickness	-0.10	0.33	0.26
Oe + Oa horizon thickness	0.20	-0.16	-0.20
B horizon sand	-0.19	-0.34	-0.04
A horizon chroma	0.27	-0.01	0.17
Eigenvalue	7.73	4.25	2.84
Broken-stick eigenvalue	3.93	2.93	2.43
% variance explained	27.6	15.2	10.2

**Note:** Values represent loadings for the first three principal components.  
\*Topographic relative moisture index.

ited loadings greater than 0.3 on the first PC of the combined environmental matrix, reflecting the complex interactions among variables and the complex structure of the environmental matrix (Table 6). However, the five highest loadings on the first PC were geomorphic variables, while the second PC was characterized by higher loadings of soil variables. These data portray the influence of geomorphology on soil properties and are consistent with the results of the CCA ordination (Fig. 2; high geomorphic correlations on the first axis, high soil correlations on the second axis) for the presence of a primary geomorphic and secondary soil gradient on this landscape.

Results of PCA combined with the range of properties occupied by the ecosystems (Tables 4 and 5) suggest that different combinations of environmental factors interact to produce similar ecosystems. For example, the hemlock–rhododendron ecosystem occupied a wide range of slope gradients from 2% on stream bottoms to more than 90% in V-shaped ravines nested on hillslopes (Table 4). By exhibiting high topographic protection and high landform indices, slopes of high gradient support mesic ecosystems even on south aspects (Table 4). On other geomorphic combinations of lower slope gradient, however, the subtle drying effects of a south aspect may result in the development of a submesic oak – mixed flora ecosystem on concave sites rather than a mesic hemlock–rhododendron ecosystem. Mean slope gradient and aspect did not differ among ecosystems in univariate analyses (Table 4), but the multivariate results demonstrate that at some constituent sites of an ecosystem, these variables strongly impact ecosystem development and the structure of the environmental complex (Table 6). Although differences in B horizon texture were important for distinguishing the two xeric ecosystems, the wide range of soil textures occupied by the mesic hemlock–rhododendron ecosystem suggests that the distribution of this ecosystem is relatively independent of soil texture (Table 5). These examples illustrate that combinations of environmental factors resulting in ecosystem development are difficult to detect using strictly univariate approaches, environmental combinations differ among constituent sites of an ecosystem type, and a given environmental factor (e.g., slope gradient) may impact ecosystem development at some constituent sites of an ecosystem type but not at other sites. Efforts to develop reliable predictive models for ecosystem distribution must account for the interacting suites of environmental complexes producing ecosystems across forest landscapes and the differential influences of the same environmental factor at different constituent sites of an ecosystem type.

### Ecosystem applications

Ecosystems classified in this study can be mapped in future research (Küchler 1967; Barnes et al. 1982; Palik et al. 2000). Map scale is a critical consideration; for example, the rare mesic hardwoods–bloodroot ecosystem occurs at fine scales of <1 ha and may need to be mapped at a finer scale than the other ecosystems. Reliable ecosystem mapping either in the field or remotely requires reliable ecosystem identification based on field characteristics and predictive models (Küchler 1967). Much of the study area consists of the xeric oak ecosystems (Table 1), and an automatically high classification success rate but an ineffective classifica-

tion could be obtained by classifying the entire landscape as the xeric oak ecosystems. Effective mapping requires consistently differentiating the landscape into xeric and mesic ecosystems and distinguishing among ecosystems within the xeric and mesic types. Challenges for field mapping include the large size of the study area, inaccessible rugged terrain, and the unreliability of global positioning system technology in the mountainous topography. Remote mapping in the study area presents several challenges because detailed vegetation and soil variables obtainable only in the field would be unavailable (existing soil surveys provide coarse data; Byrd 1963, 1972), ecosystems segregate along subtle and nonlinear gradients of environmental complexes, making accurate predictive equations difficult to develop, and existing topographic maps do not represent the topographic complexity of the landscape controlling the distribution of ecosystems. For example, none of the numerous small streams in the study area dissecting hillslopes are depicted or suggested on existing topographic maps, consistent with observations in adjacent mountain regions (Braun 1935; Morisawa 1962). Ecosystem mapping in the study area could combine the complementary approaches of field and remote mapping (Rowe and Sheard 1981; Barnes et al. 1982; Franklin 1995). With remote mapping, accuracy should be considered in the context of the ability to distinguish among the ecosystems rather than the overall classification success rate.

The ecosystem classification developed in this study provides an ecological framework in which to organize existing information (e.g., soil surveys, stand maps, rare plant locations) and in which to conduct management and future research (Barnes et al. 1982; Jose and Gillespie 1997; Pregitzer et al. 2001). For example, several hundred hectares of eastern white pine (*Pinus strobus* L.) plantations exist in the study area, and the plantations could be classified based on soils and geomorphology into their native ecosystems to guide ecosystem-specific restoration of native forests (Palik et al. 2000). Mountain laurel can proliferate and decrease tree regeneration following disturbance under reduced fire frequencies in the southern Appalachians (Monk et al. 1985; Elliott et al. 1999), and prescribed burn treatments for mountain laurel reduction could be designed specifically for the chestnut oak – mountain laurel ecosystem where mountain laurel is prevalent (Sims and Uhlig 1992). Oconee bells (*Shortia galacifolia* T. & G.) are endemic to the Jocassee Gorges region (Vivian 1967), and protection of this species is a priority in Jocassee Gorges (South Carolina Department of Natural Resources 1998). This plant occurs exclusively in the mesic hemlock–rhododendron ecosystem (Vivian 1967), and the ecosystem framework could facilitate efforts to locate additional populations. Future research in the study area, such as hydrological investigations to better understand reasons for ecosystem distribution, could be undertaken within an ecosystem framework (Yeakley et al. 1998).

**Regional comparisons**

Landform index and solum thickness were among the key variables distinguishing ecosystems classified in this study. A comparison of our results with those reported in other studies in the southern Appalachians suggests that there are some similarities but many differences (Table 7). Landform index also was cited by two other authors as a key variable,

**Table 7.** Regional comparison of ecosystem classification studies (arranged by location from south to north).

Location	Physiographic region	No. of ecosystems	Elevation (m)	Dry–moist ecosystem overstory dominants*	Major environmental variables†	Reference
Central South Carolina	Piedmont	5	120–335	<i>Quercus stellata</i> – <i>Fagus grandifolia</i>	Slope position, B horizon texture	Jones 1988
Northwest South Carolina	Upper Piedmont	4	275–550	<i>Quercus coccinea</i> – <i>Fagus grandifolia</i>	Landform index, Oe + Oa thickness	Hutto et al. 1999
Northwest South Carolina	Southern Appalachians	5	350–850	<i>Quercus coccinea</i> – <i>Tsuga canadensis</i>	Landform index, solum thickness	This study
Western North Carolina	Southern Appalachians	6	750–1525	<i>Quercus prinus</i> – <i>Quercus rubra</i>	Elevation‡, landform index	Carter et al. 2000
Western North Carolina	Southern Appalachians	5	915–1655	—§	A horizon thickness, base saturation	McNab et al. 1999
Southern Ohio	Allegheny Plateau	10	—§	<i>Quercus prinus</i> – <i>Liriodendron tulipifera</i>	Aspect, A horizon thickness	Hix and Peatry 1997

\*Dominants of the extreme dry and moist ecosystems.

†Variables cited as the most significant discriminators of ecosystems or variables strongly related to vegetation patterns.

‡No soil laboratory measurements were made.

§Data not provided in publication.

while McNab et al. (1999) reported that soil variables were most important for distinguishing ecosystems. In forests of western North Carolina at elevations higher than Jocassee Gorges, Carter et al. (2000) found that elevation primarily distinguished ecosystems. Hix and Pearcy (1997) determined that aspect largely constrained ecosystem distribution in southern Ohio, while in this study, aspect was a secondary factor differentiating ecosystems. In general, there is a wide range of different factors impacting ecosystem composition and distribution in different parts of the southern Appalachian region (Table 7). The published data suggest that caution should be used when extrapolating the importance of environmental variables far from a study area and that additional ecosystem classification studies are needed in this region to adequately describe broad patterns of ecosystem variability.

Mapping of level IV ecoregions is currently occurring in the southern Appalachians as part of the national hierarchical framework of ecological units of the United States (Cleland et al. 1997; Griffith et al. 2002). However, inadequate local data exist for many areas to reliably determine divisions for ecological units at lower hierarchical levels such as land type phases. Studies such as this one provide the local data necessary to link fine- and broad-scale mapping of hierarchical ecological units. For example, northwestern South Carolina is mapped as a single level IV ecoregion (Southern Blue Ridge Ecoregion; Griffith et al. 2002), with Jocassee Gorges located in the center. Jocassee Gorges is distinguished from surrounding areas within this ecoregion by exhibiting uniquely deep stream gorges (Mowbray and Oosting 1968) and topography more dissected by small, high-gradient streams (Cooper and Hardin 1970). These differences warrant the mapping of Jocassee Gorges as a separate ecological unit on finer-scale ecoregion maps.

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