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# Ecological species groups of South Carolina's Jocassee Gorges, southern Appalachian Mountains[1]

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ABELLA, S.R. AND V.B. SHELBURNE (Department of Forest Resources, Clemson University, Clemson, SC 29634-0331). Ecological species groups of South Carolina's Jocassee Gorges, southern Appalachian Mountains. J. Torrey Bot. Soc. 131: 220–231. 2004.—Ecological species groups, consisting of assemblages of co-occurring plant species exhibiting similar environmental affinities, were developed for ground-flora and tree strata in late-successional forests on a 13,000 ha southern Appalachian landscape. We distinguished 11 ground-flora groups that included 50 species and six tree groups comprised of 19 species. Ground-flora groups ranged from a xeric *Vaccinium* group (including *Vaccinium pallidum*, *Euphorbia corollata*, and *Piptochaetium avenaceum*) to a mesic *Rhododendron* group (typified by *Rhododendron maximum*, *Mitchella repens*, and *Hexastylis heterophylla*). Tree groups ranged from a *Quercus coccinea* group to a *Tsuga canadensis* group. Consistent with previous research, species groups exhibited a range of amplitudes from widely distributed *Smilax* and *Vitis* groups to a *Sanguinaria* group restricted to one ecosystem type. A given species group occupied a variety of different combinations of measured environmental variables, which apparently interacted to produce repeating environmental complexes across the landscape favorable for specific species groups. We also tested two multivariate methods for quantifying associations among species groups, and found that Mantel tests using traditional distance measures were inappropriate because of the double-zero problem of species absences, whereas canonical correlation modeled species group associations consistent with species distributions among sites. This study is among the first to develop ecological species groups in the southern United States, and the species group approach was useful for explaining vegetation-environment relationships, identifying groups of ground-flora and tree species that varied together across the landscape, and for determining the environmental gradients most strongly associated with species distributions.

Key words: ground-flora, vegetation distribution, ecosystem classification, Mantel test, canonical correlation.

Species-environment relationships are among the most important data needed to understand vegetation patterns on forest landscapes (Whittaker 1956, Host and Pregitzer 1992, Hix and Pearcy 1997). Developing ecological species groups, comprised of co-occurring species exhibiting similar environmental affinities, is one method to discern species-environment relationships (Mueller-Dombois and Ellenberg 1974, Host and Pregitzer 1991, Kashian et al. 2003). Ecological species groups are useful for identifying species that share similar environmental affinities and typically occupy similar sites across the landscape, and for indicating environmental complexes of forest sites based on the abundance of different species groups (Rowe 1956, Simpson et al. 1990, Goebel et al. 2001). Ecological species groups differ from individual indicator species, in that once vegetation-environment relationships are established the abundances of multiple species of a group may more strongly indicate environmental site conditions than can the abundance of individual species (Bergeron and Bouchard 1983, Spies and Barnes 1985).

Ecological species groups have been developed for a range of forest landscapes, including southern Belgium woodlands (Godart 1989), forested wetlands (Zogg and Barnes 1995), and disturbed hardwood forests of southwestern Quebec (Meilleur et al. 1992). In the eastern United States, ecological species groups have been most widely developed in Michigan as part of ecosystem classification (Spies and Barnes 1985, Archambault et al. 1989, Host and Pregitzer 1991). Ecological species groups developed in northern Michigan by Pregitzer and Barnes (1982), for example, ranged from a *Vaccinium* group (*Vaccinium angustifolium* Ait., *Epigaea repens* L., and *Gaultheria procumbens* L.) characteristic of acidic sites, to a *Viola* group (*Viola pubescens* Ait., *Adiantum pedatum* L., and *Botrychium virginianum* (L.) Sw.) typical of mesic, nutrient-rich sites. Species groups indi-

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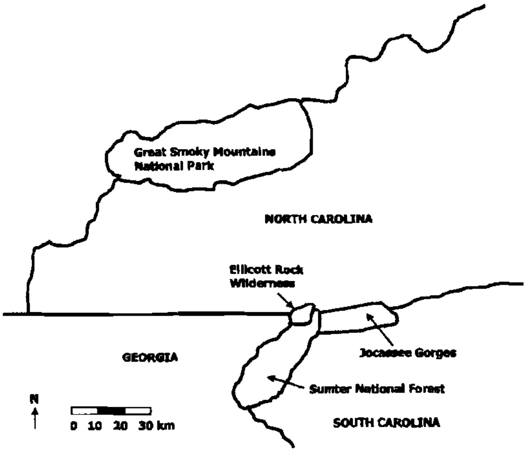

FIG. 1. Location of the 13,000 ha Jocassee Gorges, South Carolina.

cated particular environmental complexes, with soil drainage, texture, and fertility able to be inferred based on the abundance of different species groups (Pregitzer and Barnes 1982). For example, occurrences of an *Osmunda* group (*Osmunda cinnamomea* L. and *Oxalis montana* Raf.) indicated a 90% probability of soil mottling within the upper 40 cm (suggestive of a seasonally high water table), whereas occurrences of a *Viola* group indicated higher soil nitrogen and higher pH. While general habitat descriptions are available for plants in such resources as state flora manuals (Radford et al. 1968), ecological species group research provides specific data that are relatively rare for forest landscapes.

Ecological species groups have not been developed in the southern Appalachians, and the objectives of this study were (1) to develop ecological species groups as part of an ecosystem classification of a southern Appalachian landscape, and (2) to quantify associations among species groups by testing statistical methods new to ecological species group research.

**Methods.** STUDY AREA. The 13,000 ha Jocassee Gorges, managed by the South Carolina Department of Natural Resources, is in northwestern South Carolina at the southern edge of the southern Appalachian Mountains (Fig. 1). Typical elevations in the study area ranged from 350–850 m, and topography consisted of stream-dissected hillslopes. Common soils included Typic Dystrochrepts and Humic and Typic Hapludults (Byrd 1972). Presettlement vegetation was dominated by *Quercus-Castanea dentata* (Marsh.) Borkh. forests, with *Tsuga canadensis* (L.) Carr. and mesic hardwood forests forming inclusions in riparian and topographically protected areas (Holmes 1911, Braun 1950). In a recent ecosystem classification of the study area, we identified five major ecosystem types, distinguished by differences in geomorphology, soils, and late-successional vegetation (Abella et al. 2003). Xeric *Quercus/Vaccinium* ecosystems occupied ridgetops and other dry sites, and were typified by *Quercus coccinea* Muenchh., *Quercus velutina* Lam., and *Vaccinium pallidum* Ait. Xeric *Quercus prinus/Kalmia* ecosystems inhabited upper slope positions on north aspects or soils more rocky than the *Quercus/Vaccinium* ecosystem. Submesic *Quercus*/mixed flora ecosystems were typified by combinations of *Quercus alba* L., *Carya alba* (L.) Nutt. ex Ell., *Magnolia fraseri* Walt., and *Thelypteris noveboracensis* (L.) Nieuwl. Although rare, mesic hardwoods/*Sanguinaria* ecosystems exhibited the highest ground-flora diversity and occupied the deepest soils (sola $>$ 100 cm thick). Mesic *Tsuga/Rhododendron* ecosystems dominated riparian areas and were characterized by *T. canadensis*, *Rhododendron maximum* L., and *Leucothoe fontanesiana* (Steud.) Sleumer.

FIELD PROCEDURES. To develop the ecosystem classification, we sampled vegetation, soils, and geomorphology on 48, 0.1 ha (20 × 50 m) plots distributed across the landscape in forests greater than age 70 yr following methods in Abella et al. (2003). A total of 28 soil and geomorphic variables were measured on each plot, and among the most important of these variables were landform index (McNab 1993) and the topographic relative moisture index (Parker 1982). Landform index quantifies site protection by surrounding topography, with higher indices indicating greater topographic protection usually associated with moist sites. The topographic relative moisture index integrates slope aspect, slope gradient, slope shape, and topographic features and ranges from 0–100, with higher indices indicating greater potential moisture availability. Soil variables determined for both A and B horizons included texture, organic C, pH, Munsell color, and horizon thickness.

Each 0.1 ha plot was divided into ten 0.01 ha subplots for vegetation sampling, and we categorized the areal percent cover of each plant species rooted in each subplot using the cover classes of Peet et al. (1998): 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–

Table 1. Importance values and frequencies of species for ground-flora ecological species groups for forest ecosystems of Jocassee Gorges, South Carolina. Values in bold-face type represent the ecosystem types in which a species group was most important.

| | Ecosystem type[a] | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | X Q/V | | X Q/K | | S Q/MF | | M H/S | | M T/R | |
| Species group[b] | IV[c] | Q[c] | IV | Q | IV | Q | IV | Q | IV | Q |
| *Vaccinium* group | | | | | | | | | | |
| *Vaccinium pallidum*—low-bush blueberry | **5.2 ± 3.0** | **100** | 3.7 ± 2.4 | 86 | 0.4 ± 0.5 | 44 | — | — | 0.1 ± 0.1 | 7 |
| *Sassafras albidum*—sassafras | **2.6 ± 1.5** | **100** | 1.4 ± 0.7 | 71 | 0.7 ± 0.7 | 89 | 0.1 ± 0.1 | 33 | 0.1 ± 0.1 | 7 |
| *Euphorbia corollata*—flowering spurge | **1.4 ± 1.2** | **71** | 0.2 ± 0.4 | 29 | 0.3 ± 0.5 | 33 | — | — | — | — |
| *Piptochaetium avenaceum*—needle grass | **1.2 ± 2.0** | **43** | — | — | — | — | — | — | — | — |
| *Arundinaria* group | | | | | | | | | | |
| *Arundinaria gigantea*—cane | **3.8 ± 1.8** | **93** | **2.7 ± 1.6** | **86** | **2.7 ± 1.7** | **89** | 1.1 ± 1.0 | 67 | 0.7 ± 1.0 | 53 |
| *Quercus coccinea/Q. velutina*—scarlet/black oak | **6.5 ± 2.2** | **100** | **3.1 ± 2.1** | **86** | **2.1 ± 1.8** | **78** | 1.4 ± 0.6 | 100 | 0.4 ± 0.8 | 27 |
| *Chimaphila maculata*—pipsissewa | **2.9 ± 1.7** | **100** | **1.9 ± 2.0** | **100** | **1.0 ± 1.0** | **78** | 0.1 ± 0.1 | 33 | 0.7 ± 0.7 | 80 |
| *Nyssa sylvatica*—blackgum | **4.1 ± 1.6** | **100** | **1.9 ± 2.0** | **86** | **1.5 ± 0.8** | **100** | 0.9 ± 1.0 | 100 | 0.4 ± 0.7 | 40 |
| *Oxydendrum arboreum*—sourwood | **1.8 ± 0.9** | **100** | **1.8 ± 1.3** | **100** | **0.8 ± 0.4** | **100** | — | — | 0.4 ± 0.4 | 60 |
| *Kalmia* group | | | | | | | | | | |
| *Kalmia latifolia*—mountain laurel | 4.5 ± 3.5 | 86 | **7.5 ± 3.1** | **100** | 2.2 ± 1.7 | 89 | — | — | 1.2 ± 2.0 | 60 |
| *Quercus prinus*—chestnut oak | 3.0 ± 2.1 | 79 | **4.1 ± 1.7** | **100** | 1.3 ± 0.8 | 100 | 0.1 ± 0.1 | 33 | 0.6 ± 0.8 | 47 |
| *Gaylussacia ursina*—bear huckleberry | 2.5 ± 2.5 | 71 | **2.9 ± 1.2** | **100** | 1.4 ± 1.9 | 44 | — | — | 0.8 ± 0.9 | 53 |
| *Chamaelirium luteum*—devil's-bit | 0.6 ± 1.1 | 29 | **0.6 ± 0.8** | **43** | 0.6 ± 0.9 | 56 | — | — | 0.2 ± 0.5 | 27 |
| *Galax urceolata*—galax | 0.2 ± 0.6 | 21 | **2.4 ± 2.6** | **71** | 0.6 ± 0.9 | 56 | — | — | 0.8 ± 1.3 | 47 |
| *Rhododendron minus*—Piedmont rhododendron | 0.1 ± 0.5 | 7 | **1.0 ± 1.3** | **57** | 0.1 ± 0.3 | 22 | — | — | 0.6 ± 1.4 | 47 |
| *Smilax* group | | | | | | | | | | |
| *Smilax rotundifolia*—greenbrier | **5.4 ± 0.8** | **100** | **4.7 ± 1.3** | **100** | **3.1 ± 0.5** | **100** | **2.1 ± 0.4** | **100** | **3.2 ± 1.3** | **100** |
| *Acer rubrum*—red maple | **5.8 ± 1.0** | **100** | **4.7 ± 1.0** | **100** | **3.2 ± 0.8** | **100** | **2.3 ± 0.4** | **100** | **3.0 ± 0.9** | **100** |
| *Carya glabra/C. alba*—hickory | **3.9 ± 1.5** | **100** | **2.7 ± 1.8** | **86** | **2.5 ± 0.9** | **100** | **3.2 ± 0.2** | **100** | **1.6 ± 1.1** | **87** |
| *Magnolia fraseri*—Fraser magnolia | **2.5 ± 1.7** | **86** | **1.5 ± 1.6** | **71** | **2.3 ± 1.4** | **100** | **1.0 ± 0.5** | **100** | **0.6 ± 0.6** | **53** |
| *Vitis* group | | | | | | | | | | |
| *Vitis rotundifolia*—muscadine | **3.1 ± 1.9** | **93** | **1.9 ± 0.8** | **100** | **3.0 ± 1.0** | **100** | **2.2 ± 0.6** | **100** | **3.2 ± 0.9** | **100** |
| *Goodyera pubescens*—rattlesnake plantain | **0.8 ± 0.6** | **79** | **1.4 ± 1.4** | **100** | **1.3 ± 0.6** | **89** | **0.8 ± 0.7** | **100** | **1.6 ± 1.0** | **100** |
| *Pyrularia pubera*—buffalo nut | **1.7 ± 2.4** | **43** | **1.3 ± 2.3** | **29** | **1.1 ± 1.8** | **33** | **1.0 ± 1.7** | **33** | **2.0 ± 1.6** | **80** |
| *Thelypteris* group | | | | | | | | | | |
| *Thelypteris noveboracensis*—New York fern | 0.4 ± 0.8 | 36 | 1.2 ± 1.9 | 43 | **3.5 ± 2.1** | **89** | **2.2 ± 1.2** | **100** | 1.8 ± 1.6 | 80 |
| *Halesia carolina*—Carolina silverbell | 0.2 ± 0.4 | 14 | 0.5 ± 1.1 | 29 | **2.2 ± 1.7** | **89** | **3.1 ± 0.4** | **100** | 0.8 ± 0.8 | 67 |
| *Toxicodendron radicans*—poison ivy | 0.2 ± 0.4 | 21 | 0.1 ± 0.2 | 14 | **1.5 ± 1.6** | **78** | **2.6 ± 0.6** | **100** | 1.8 ± 1.3 | 80 |
| *Polygonatum biflorum*—Solomon's-seal | 0.2 ± 0.3 | 29 | 0.6 ± 0.7 | 57 | **0.6 ± 0.7** | **89** | **0.9 ± 0.8** | **67** | 0.8 ± 0.8 | 80 |

Table 1. Continued.

| | Ecosystem type[a] | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | X Q/V | | X Q/K | | S Q/MF | | M H/S | | M T/R | |
| Species group[b] | IV[c] | Q[c] | IV | Q | IV | Q | IV | Q | IV | Q |
| *Polystichum* group | | | | | | | | | | |
| *Polystichum acrostichoides*—Christmas fern | 0.8 ± 1.2 | 50 | 3.6 ± 1.8 | 100 | **3.4 ± 0.7** | **100** | **3.2 ± 0.1** | **100** | **4.3 ± 1.5** | **93** |
| *Euonymus americana*—strawberry-bush | 0.2 ± 0.4 | 29 | 0.5 ± 0.7 | 57 | **1.2 ± 0.8** | **78** | **1.4 ± 0.3** | **100** | **2.0 ± 1.3** | **87** |
| *Parthenocissus quinquefolia*—Virginia creeper | 1.0 ± 1.3 | 64 | 0.4 ± 0.6 | 43 | **2.6 ± 0.7** | **100** | **3.1 ± 0.6** | **100** | **2.4 ± 1.2** | **87** |
| *Hydrangea arborescens*—wild hydrangea | 0.1 ± 0.1 | 7 | 1.0 ± 1.1 | 71 | **1.2 ± 0.9** | **78** | **1.1 ± 0.8** | **100** | **0.9 ± 1.1** | **60** |
| *Sanguinaria* group | | | | | | | | | | |
| *Sanguinaria canadensis*—bloodroot | — | — | — | — | 0.1 ± 0.3 | 22 | **1.9 ± 0.5** | **100** | 0.3 ± 0.6 | 33 |
| *Caulophyllum thalictroides*—blue cohosh | — | — | — | — | — | — | **1.1 ± 0.8** | **100** | — | — |
| *Panax quinquefolius*—ginseng | — | — | — | — | 0.1 ± 0.1 | 11 | **0.3 ± 0.3** | **67** | — | — |
| *Adiantum* group | | | | | | | | | | |
| *Adiantum pedatum*—maidenhair fern | — | — | — | — | 0.1 ± 0.1 | 22 | **1.4 ± 0.7** | **100** | 0.4 ± 0.7 | 33 |
| *Actaea pachypoda*—white baneberry | — | — | — | — | — | — | **1.2 ± 1.1** | **67** | 0.3 ± 0.6 | 27 |
| *Botrychium virginianum*—rattlesnake fern | — | — | 0.1 ± 0.2 | 14 | 0.1 ± 0.2 | 22 | **1.1 ± 0.8** | **100** | 0.5 ± 0.6 | 53 |
| *Aralia racemosa*—spikenard | — | — | — | — | — | — | **0.5 ± 0.5** | **67** | 0.1 ± 0.3 | 27 |
| *Sanicula candensis*—snakeroot | — | — | — | — | 0.1 ± 0.1 | 33 | **1.6 ± 0.9** | **100** | 0.6 ± 0.7 | 60 |
| *Tiarella* group | | | | | | | | | | |
| *Tiarella cordifolia*—foamflower | — | — | — | — | 0.2 ± 0.4 | 33 | **2.2 ± 0.6** | **100** | **1.8 ± 1.2** | **80** |
| *Phegopteris hexagonoptera*—broad beech-fern | — | — | — | — | 0.7 ± 0.8 | 67 | **2.2 ± 1.6** | **100** | **1.3 ± 1.4** | **67** |
| *Medeola virginiana*—Indian cucumber-root | 0.1 ± 0.3 | 7 | 0.1 ± 0.2 | 29 | 0.7 ± 0.8 | 56 | **1.4 ± 0.9** | **100** | **1.2 ± 1.2** | **73** |
| *Arisaema triphyllum*—jack-in-the-pulpit | 0.1 ± 0.1 | 14 | — | — | 1.6 ± 0.5 | 100 | **1.8 ± 0.4** | **100** | **1.9 ± 0.9** | **100** |
| *Rhododendron* group | | | | | | | | | | |
| *Rhododendron maximum*—rosebay rhododendron | 0.4 ± 1.2 | 14 | 3.1 ± 4.2 | 71 | 1.1 ± 1.5 | 56 | 0.3 ± 0.4 | 67 | **5.5 ± 6.4** | **100** |
| *Leucothoe fontanesiana*—doghobble | 0.1 ± 0.5 | 7 | — | — | 0.1 ± 0.2 | 22 | 0.6 ± 1.1 | 33 | **3.6 ± 2.5** | **87** |
| *Mitchella repens*—partridge berry | 0.1 ± 0.3 | 14 | 0.4 ± 0.6 | 57 | 1.2 ± 0.9 | 89 | 1.7 ± 0.6 | 100 | **3.3 ± 1.3** | **100** |
| *Hexastylis heterophylla/H. shuttleworthii* | 0.1 ± 0.6 | 7 | 0.6 ± 1.0 | 29 | 0.4 ± 0.8 | 44 | — | — | **2.5 ± 2.6** | **67** |
| *Tsuga canadensis*—eastern hemlock | 0.2 ± 0.4 | 29 | 1.1 ± 1.3 | 57 | 0.6 ± 1.0 | 44 | 1.0 ± 1.1 | 67 | **3.4 ± 1.4** | **100** |

[a] Abbreviations for ecosystem types are as follows: X Q/V = xeric *Quercus/Vaccinium*, X Q/K = xeric *Quercus prinus/Kalmia*, S Q/MF = submesic *Quercus*/mixed flora, M H/S = mesic hardwoods/*Sanguinaria*, and M T/R = mesic *Tsuga/Rhododendron*.

[b] Tree species are seedlings and saplings <1 cm diameter at 1.4 m.

[c] IV = importance value (average of relative cover class and relative frequency). Q = percent frequency at a 0.1 ha plot scale. Importance values are mean ± SD and do not sum to 100 for an ecosystem type because not all sampled species were included in a species group.

95%, 10 = > 95%. These measurements were made for all vascular plant species including tree species less than 1 cm diameter at 1.4 m; this stratum is termed ground-flora throughout this paper. Trees greater than 1 cm diameter were inventoried by species and diameter on each plot, and are termed trees in this paper. Nomenclature follows Kartesz (1999).

Statistical Analyses. We developed ecological species groups separately for ground-flora and tree strata in an R-mode analysis (Legendre and Legendre 1998) using cluster analysis (Euclidean distance, Ward's linkage method) and non-metric multidimensional scaling (default settings, 50 randomized runs [McCune and Mefford 1999]). Importance values for ground-flora ([relative frequency + relative cover class]/2) and trees ([relative density + relative basal area]/2) were used in analyses. Following widely used procedures for developing ecological species groups, raw plot × species and plot × environmental variable matrices were examined in combination with results of multivariate analyses to develop species groups (Mueller-Dombois and Ellenberg 1974, Archambault et al. 1989, Kashian et al. 2003). Species that typically occupied the same plots and were abundant on similar environmental complexes were identified by their proximity on ordination diagrams, cluster analysis groupings, and by examining species-environment correlations in raw data matrices. Fifty ground-flora species were included in 11 ground-flora groups and 19 tree species were included in six tree species groups. While the number of species included in groups, the number of groups, and the assignment of species to groups in this study resulted in robust species groups, it should be recognized that different groups and numbers of groups equally logical could also result depending on such factors as the areal scale of analysis (smaller or larger than the 0.1 ha plot scale in this study), measure of species quantity (presence/absence versus different quantitative measures), and the environmental variables measured.

We examined associations between species groups using Mantel tests (Mantel 1967) and canonical correlation (Gittins 1985, Tabachnick and Fidell 1996). Species group-species group associations have previously been described qualitatively (Host and Pregitzer 1991), and our goal in Mantel tests and canonical correlation was to test methods for quantifying species group associations. For Mantel tests, one multivariate distance matrix (48 plots × 48 plots) was computed for each species group using Sørensen dissimilarity distances in PC-ORD (McCune and Mefford 1999). Distance matrices were compared between each pair of species groups with the standardized Mantel statistic (interpretation similar to Pearson's $r$), and significance of correlations was determined by permutation (9999 permutations). Comparisons of ecological species group associations in this study are similar to comparisons using Mantel tests of plant taxonomic groups in Amazonian rain forests by Tuomisto et al. (1995), and to comparisons of plant life-form groups in McCune and Grace (2002). Canonical correlation quantifies the correlation between two sets of variables, with the sets of variables in this study consisting of the constituent species of two species groups. Linear combinations (canonical variates) of the variables of each set are calculated, and the association between the pairs of canonical variates is the canonical correlation which ranges from $-1$ to $+1$ (Khattree and Naik 2000). We computed a matrix (69 × 69) of Spearman rank correlations between each pair of individual species and ran canonical correlation from this matrix for a partial nonparametric canonical correlation. Only the first canonical variate was typically needed for interpretation, and for significant associations we inspected species correlations with each variate to determine positive or negative association among species groups.

Relationships among species groups and environmental variables were investigated using point-biserial correlation, a method that correlates a binary variable with a continuous variable. Kent and Coker (1992) note that point-biserial correlation has been rarely used in vegetation studies, but the method is useful when there are many zeros in a data set resulting from species absences typical of vegetation data. In this study, the binary variable was an above/below the median importance value division for each species group, and the continuous variable was an environmental variable. Importance values of constituent species of a species group were averaged for each plot for these analyses.

**Results and Discussion.** Ground-flora Species Groups. We distinguished 11 ground-flora species groups, with each group consisting of species exhibiting similar distributions among ecosystems (Table 1). Groups ranged from a xeric *Vaccinium* group exemplified by *V. pallidum* and *Piptochaetium avenaceum* (L.) Parodi, to a mesic *Rhododendron* group typified by *R. maximum* and *Mitchella repens* L. The *Arundinaria* group consisted of species such as *A. gigantea* (Walt.) Muhl. and *Chimaphila maculata* (L.) Pursh that were widespread but most common in xeric ecosystems. Dominating the xeric *Quercus prinus*/*Kalmia* ecosystem, species like *Kalmia latifolia* L. and *Gaylussacia ursina* (M.A. Curtis) Torr. & Gray ex Gray of the *Kalmia* group also were common in the xeric *Quercus*/*Vaccinium* and submesic *Quercus*/mixed flora ecosystems. *Acer rubrum* L. and species of the *Smilax* group were common in all ecosystems, but this group was less common in the mesic *Tsuga*/*Rhododendron* ecosystem. The *Vitis* group, typified by *V. rotundifolia* Michx. and *Goodyera pubescens* (Willd.) R. Br. ex Ait. f., exhibited little environmental preference.

*Thelypteris noveboracensis*, *Halesia carolina* L., and other species of the *Thelypteris* group were sparse in xeric ecosystems and most dominant in the submesic *Quercus*/mixed flora and mesic hardwoods/*Sanguinaria* ecosystems. The *Polystichum* group, characterized by such species as *Polystichum acrostichoides* (Michx.) Schott and *Euonymus americana* L., was widely distributed but dominant only in submesic-mesic ecosystems. *Sanguinaria canadensis* L., *Caulophyllum thalictroides* (L.) Michx., and *Panax quinquefolius* L. comprising the *Sanguinaria* group exhibited the narrowest distribution and were largely restricted to the mesic hardwoods/*Sanguinaria* ecosystem. Species of the *Tiarella* group, such as *Tiarella cordifolia* L. and *Medeola virginiana* L., were abundant in submesic and mesic ecosystems but most dominant in the mesic hardwoods/*Sanguinaria* ecosystem. Members of the *Rhododendron* group, like *Leucothoe fontanesiana*, *Hexastylis heterophylla* (Ashe) Small, *Hexastylis shuttleworthii* (Britten & Baker) Small, and *Tsuga canadensis* seedlings, were sparse in xeric ecosystems and dominated the mesic *Tsuga*/*Rhododendron* ecosystem.

With the exception of the *Sanguinaria* group restricted to the mesic hardwoods/*Sanguinaria* ecosystem, species groups occurred in multiple ecosystems but were typically quantitatively most important in three or fewer ecosystems (Table 1). These results support the conclusions of species group studies in Michigan. For example, Archambault et al. (1989) found that a *Thalictrum* group (dominated by *Thalictrum dioicum* L., *Viola pubescens*, and *Viburnum acerifolium* L.) occurred in several southeastern Michigan *Quercus* ecosystems, but was most common in an ecosystem with moist, loamy soils containing *Quercus rubra* L. Likewise, Host and Pregitzer (1991) classified nine species groups in upland ecosystems of northwestern lower Michigan and reported a range of group amplitudes from a specific *Osmorhiza* group (constituents included *Osmorhiza claytonii* (Michx.) C.B. Clarke and *Viola canadensis* L.), to a broad *Viburnum* group (*V. acerifolium*, *Aralia nudicaulis* L., and *Mitchella repens*).

TREE SPECIES GROUPS. We formed six groups of tree species (> 1 cm diameter) comprised of 19 of the 35 tree species recorded in this study (Table 2). Similar to the ground-flora groups, tree groups did not exclusively occur in one ecosystem but all groups were quantitatively most dominant in fewer than three ecosystems. *Quercus coccinea*, *Q. velutina*, and *Nyssa sylvatica* Marsh. of the *Quercus coccinea* group, for example, totaled a mean importance value of 31 in the xeric *Quercus*/*Vaccinium* ecosystem and never totaled an importance value more than eight in any other ecosystem. *Quercus prinus* L. dominated the xeric *Quercus prinus*/*Kalmia* ecosystem and also was common in the xeric *Quercus*/*Vaccinium* and submesic ecosystems. The distribution of the *Quercus alba* group (including *Carya* and *Magnolia fraseri*) was difficult to characterize, although this group was most abundant in the submesic *Quercus*/mixed flora ecosystem. *Liriodendron tulipifera* L., *Halesia carolina*, and *Quercus rubra* of the *Liriodendron tulipifera* group dominated the mesic hardwoods/*Sanguinaria* ecosystem, totaling a mean importance value of 46. The *Tsuga canadensis* group was diverse and most dominant in the mesic *Tsuga*/*Rhododendron* ecosystem.

ASSOCIATIONS WITH ENVIRONMENTAL VARIABLES. Based on point-biserial correlation, landform and soil thickness variables were more closely associated with species group distribution than were slope aspect, soil texture, pH, and organic C. Little correlation between species groups and soil texture, pH, and organic C in this study contrasts sharply with the results of Michigan studies, where these soil variables have formed dominant gradients associated with species group distribution (Pregitzer and Barnes 1982, Spies and Barnes 1985, Archambault et al. 1989). When environmental variables were partitioned into above/below the median importance value divisions for species groups, landform index (measures site protection), A-horizon thickness, and the topographic relative moisture index were

Table 2. Importance values and frequencies of species for tree ecological species groups for forest ecosystems of Jocassee Gorges, South Carolina. Values in boldface type represent the ecosystem types in which a species group was most important.

| | Ecosystem type[a] | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | X Q/V | | X Q/K | | S Q/MF | | M H/S | | M T/R | |
| Species group | IV[b] | Q[b] | IV | Q | IV | Q | IV | Q | IV | Q |
| *Quercus coccinea* group | | | | | | | | | | |
| *Quercus coccinea*—scarlet oak | **11 ± 9** | **86** | 1 ± 2 | 43 | 1 ± 2 | 11 | — | — | — | — |
| *Quercus velutina*—black oak | **6 ± 8** | **71** | 2 ± 3 | 57 | 4 ± 5 | 56 | — | — | <1 | 7 |
| *Nyssa sylvatica*—blackgum | **14 ± 7** | **100** | 5 ± 4 | 100 | 3 ± 2 | 89 | <1 | 33 | 1 ± 2 | 47 |
| *Oxydendrum arboreum* group | | | | | | | | | | |
| *Oxydendrum arboreum*—sourwood | **10 ± 4** | **100** | **9 ± 4** | **100** | 6 ± 3 | 100 | <1 | 33 | 2 ± 3 | 80 |
| *Cornus florida*—flowering dogwood | **3 ± 3** | **79** | **5 ± 3** | **100** | 4 ± 3 | 100 | 5 ± 6 | 67 | 1 ± 2 | 60 |
| *Acer rubrum*—red maple | **22 ± 6** | **100** | **23 ± 4** | **100** | 18 ± 6 | 100 | 16 ± 6 | 100 | 11 ± 8 | 100 |
| *Quercus prinus* group | | | | | | | | | | |
| *Quercus prinus*—chestnut oak | 8 ± 10 | 79 | **33 ± 12** | **100** | 8 ± 8 | 67 | — | — | 2 ± 5 | 40 |
| *Quercus alba* group | | | | | | | | | | |
| *Quercus alba*—white oak | 10 ± 9 | 93 | — | — | **13 ± 11** | **89** | — | — | 4 ± 6 | 60 |
| *Carya glabra/C. alba*—hickory | 5 ± 7 | 100 | 6 ± 6 | 86 | **9 ± 4** | **100** | 8 ± 6 | 100 | 5 ± 6 | 87 |
| *Magnolia fraseri*—Fraser magnolia | 1 ± 1 | 50 | <1 | 29 | **4 ± 5** | **100** | 1 ± 1 | 100 | 1 ± 2 | 67 |
| *Liriodendron tulipifera* group | | | | | | | | | | |
| *Liriodendron tulipifera*—tulip-poplar | 3 ± 5 | 71 | 3 ± 3 | 71 | 10 ± 6 | 100 | **35 ± 16** | **100** | 11 ± 5 | 100 |
| *Halesia carolina*—Carolina silverbell | <1 | 7 | 1 ± 2 | 14 | 4 ± 5 | 67 | **10 ± 5** | **100** | 1 ± 2 | 53 |
| *Quercus rubra*—northern red oak | <1 | 7 | 1 ± 2 | 14 | 3 ± 5 | 33 | **<1** | **33** | 2 ± 2 | 53 |
| *Tsuga canadensis* group | | | | | | | | | | |
| *Tsuga canadensis*—eastern hemlock | <1 | 43 | 6 ± 9 | 71 | 4 ± 5 | 89 | 6 ± 8 | 67 | **34 ± 16** | **100** |
| *Betula lenta*—sweet birch | <1 | 7 | <1 | 29 | 1 ± 1 | 44 | 2 ± 1 | 100 | **6 ± 6** | **93** |
| *Fagus grandifolia*—American beech | <1 | 14 | <1 | 29 | 2 ± 4 | 44 | 3 ± 6 | 33 | **4 ± 4** | **80** |
| *Pinus strobus*—eastern white pine | 1 ± 2 | 50 | — | — | 1 ± 2 | 56 | — | — | **4 ± 7** | **47** |
| *Tilia americana*—American basswood | — | — | — | — | 1 ± 2 | 22 | 6 ± 7 | 67 | **3 ± 5** | **60** |

[a] Abbreviations for ecosystem types are as follows: X Q/V = xeric *Quercus/Vaccinium*, X Q/K = xeric *Quercus prinus/Kalmia*, S Q/MF = submesic *Quercus*/mixed flora, M H/S = mesic hardwoods/*Sanguinaria*, and M T/R = mesic *Tsuga/Rhododendron*.

[b] IV = importance value (average of relative density and relative basal area). Q = percent frequency at a 0.1 ha plot scale. Importance values are mean ± SD and do not sum to 100 for an ecosystem type because not all sampled species were included in a species group.

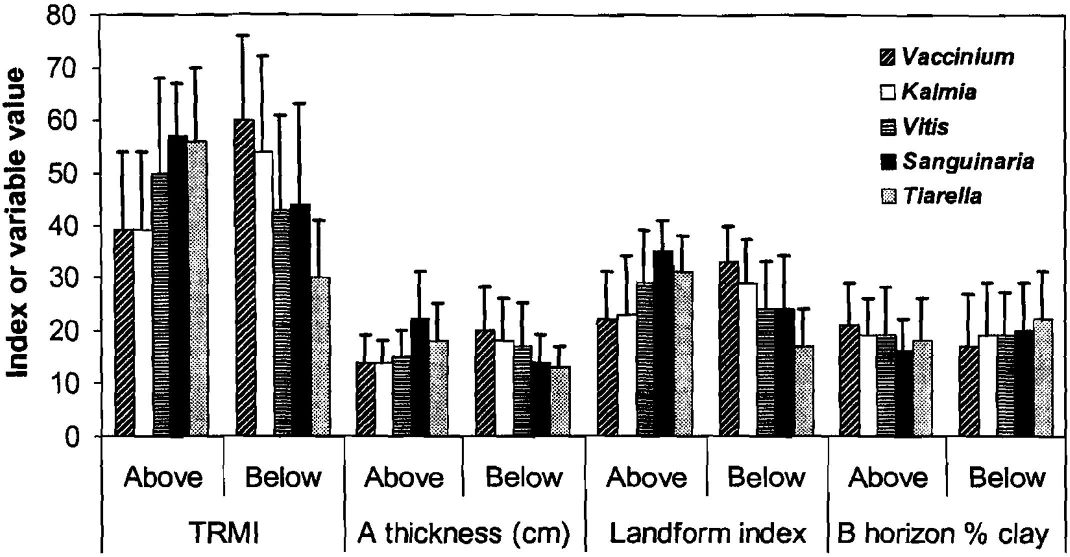

FIG. 2. Mean values of major environmental variables when species groups are more or less abundant than their median abundance (above and below median importance values) for five ecological species groups representative of the range of species groups for Jocassee Gorges, South Carolina. Higher topographic relative moisture indices (TRMI) indicate greater potential moisture availability; higher landform indices indicate greater topographic protection. Error bars are 1 SD.

lower when xeric groups such as the *Vaccinium* group were above their median importance (Fig. 2). In contrast, mesic groups such as the *Sanguinaria* group were more prevalent at higher landform indices (greater site protection), thicker A horizons, and larger moisture indices (higher potential moisture).

Species groups generally were not associated with one specific landform or soil characteristic (Table 3). With the exception of a widespread *Vitis* group not associated with any environmental complex, a given species group occurred on different combinations of environmental variables that apparently interacted to produce an environmental complex favorable for that group. For example, the *Vaccinium* group dominated xeric sites, but these xeric sites could occur on a south-facing upper hillslope or on a dry, convex nose slope embedded on a predominately moist north aspect. Tree species groups also occupied different combinations of environmental variables, and were as specific or more specific than ground-flora groups in their requirements of environmental complexes. There was no widespread tree group uncharacteristic of any environmental complex equivalent to the non-preferential *Vitis* ground-flora group. Trees have traditionally not been included in species group research, probably partly because fewer tree species occur on many northern landscapes where most species group research has occurred (Kashian et al. 2003), and it is thought that trees do not reflect site conditions as specifically as ground-flora. In late-successional forests with diverse tree composition such as in the southern Appalachians, however, forming tree species groups is likely to be useful for understanding vegetation-environment relationships for different forest strata. A practical application of tree groups could be to develop species groups along successional sequences to predict how species-environment relationships change on different environmental sites after disturbance, or whether characteristic species groups occur at different times after different types of disturbance.

ASSOCIATIONS AMONG SPECIES GROUPS. Relationships among species groups typically are described only qualitatively in species group research (e.g., Host and Pregitzer 1991). Many other types of ecological research also require descriptions of associations among different groups of species, and we tested Mantel tests for their ability to quantify species group associations. Mantel tests previously have been used to examine associations among plant taxonomic groups (Tuomisto et al. 1995) and plant growth forms (McCune and Grace 2002). We tabulated results of Mantel tests for quantifying ecological species group associations in this study in a 17

Table 3. Characteristic environmental complexes of ecological species groups of Jocassee Gorges, South Carolina.

| Species group | Characteristic combinations of environmental complexes |
|---|---|
| Ground-flora groups | |
| *Vaccinium* | South aspects, upper slope positions, ridgetops and nose slopes; xeric sites |
| *Arundinaria* | Widespread but most dominant on south aspects and upper slope positions; xeric sites |
| *Kalmia* | North aspects or rocky south aspects, upper slope positions; xeric-subxeric sites |
| *Smilax* | Widespread but typically most dominant on xeric-submesic sites |
| *Vitis* | Widespread; not characteristic of any environmental complex |
| *Thelypteris* | Concave landforms (3-sided coves, stream ravines); submesic sites |
| *Polystichum* | Stream ravines and bottoms, hillslopes of north aspects; submesic-mesic sites |
| *Sanguinaria* | Thick soil sola (>100 cm), A-horizon pH > 5, A-horizon organic C > 5%; mesic sites |
| *Adiantum* | Thick soil sola (>100 cm), A-horizon pH > 5, A-horizon organic C > 5%; mesic sites |
| *Tiarella* | Thick soil sola (>100 cm), stream ravines, bottoms, north aspects; mesic sites |
| *Rhododendron* | Stream ravines, bottoms, hillslopes of high slope gradient (>60%); mesic sites |
| Tree groups | |
| *Quercus coccinea* | B-horizon clay > 20%; south aspects, upper slope positions; ridgetops; xeric sites |
| *Oxydendrum arboreum* | Widespread but most dominant on upper slope positions; xeric-submesic sites |
| *Quercus prinus* | Rocky upper slope positions, north aspects, high slope gradients (>60%); subxeric sites |
| *Quercus alba* | Stream ravines and 3-sided coves of submesic sites; occasionally dominant on xeric sites |
| *Liriodendron tulipifera* | Thick soil sola (>100 cm); 3-sided coves, stream ravines, bottoms; submesic-mesic sites |
| *Tsuga canadensis* | Stream ravines, bottoms, north aspects, high slope gradients (>60%); mesic sites |

× 17 group association matrix corresponding to the 11 ground-flora and six tree groups. However, species groups that never occurred together ecologically were consistently determined by the Mantel test to be positively associated. For example, the xeric *Vaccinium* group was most positively associated with the mesic *Tiarella* group ($r = 0.41$, $P < 0.0001$) even though these groups did not exhibit distributional overlap (Table 1). This discrepancy occured because of the double-zero problem described by Legendre and Legendre (1998), where species absences are weighted the same as species occurrences. Consider a hypothetical example of two plots on xeric ridgetops, with both plots containing species of the xeric *Vaccinium* group and consequently exhibiting high similarity in the multivariate distance matrix computed using the *Vaccinium* group. Species of the mesic *Tiarella* group do not occur on these xeric plots, but in the distance matrix computed from the *Tiarella* group these plots would be similar only because the plots share no species. Because of these shared zeros, the *Vaccinium* and *Tiarella* groups exhibit positive association in a Mantel test. Unless this double-zero problem is accounted for in the distance measure used to compute the distance matrix, Mantel tests incorrectly return positive association when no association or negative association should occur. Mantel tests can use any distance measure (McCune and Grace 2002), and experimentation is needed to evaluate methods to account for the double-zero problem if Mantel tests are to be used to quantify species group associations.

In contrast to Mantel tests that are based on multivariate plot dissimilarities, canonical correlation directly quantifies the association between combinations of two sets of variables such as groups of species (Gittins 1985, Tabachnick and Fidell 1996). Results suggest canonical correlation modeled species group associations consistent with abundances of species among sites (Table 4). Rather than being the

Table 4. Matrix of canonical correlations of ground-flora and tree ecological species groups of Jocassee Gorges, South Carolina. Values in bold-face type are significant at $P < 0.05$.

| | VAC[a] | ARU | KAL | SMI | VIT | THE | POL | SAN | ADI | TIA | RHO | QC | OA | QP | QA | LT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ARU | **0.94** | 1 | | | | | | | | | | | | | | |
| KAL | **0.84** | **0.82** | 1 | | | | | | | | | | | | | |
| SMI | **0.85** | **0.89** | **0.76** | 1 | | | | | | | | | | | | |
| VIT | **−0.48** | −0.50 | **−0.60** | **−0.61** | 1 | | | | | | | | | | | |
| THE | **−0.79** | **−0.71** | **−0.74** | **−0.86** | 0.45 | 1 | | | | | | | | | | |
| POL | **−0.82** | **−0.88** | **−0.81** | **−0.84** | **0.51** | **0.75** | 1 | | | | | | | | | |
| SAN | −0.52 | **−0.62** | −0.54 | **−0.72** | 0.35 | **0.64** | 0.52 | 1 | | | | | | | | |
| ADI | −0.58 | **−0.70** | −0.65 | **−0.70** | 0.46 | **0.67** | **0.68** | **0.77** | 1 | | | | | | | |
| TIA | **−0.83** | **−0.83** | **−0.81** | **−0.85** | 0.47 | **0.85** | **0.80** | **0.65** | **0.73** | 1 | | | | | | |
| RHO | **−0.92** | **−0.89** | **−0.81** | **−0.84** | **0.65** | **0.78** | **0.79** | 0.54 | **0.68** | **0.83** | 1 | | | | | |
| QC | **0.86** | **0.89** | **0.79** | **0.80** | **−0.51** | **−0.77** | **−0.84** | −0.46 | **−0.72** | **−0.81** | **−0.77** | 1 | | | | |
| OA | **0.76** | **0.82** | **0.90** | **0.74** | −0.51 | **−0.73** | **−0.73** | **−0.56** | **−0.73** | **−0.81** | **−0.79** | **0.72** | 1 | | | |
| QP | **0.57** | **0.49** | **0.88** | 0.30 | **−0.45** | **−0.50** | **−0.66** | −0.33 | **−0.48** | **−0.53** | **−0.70** | 0.32 | **0.48** | 1 | | |
| QA | **0.58** | **−0.54** | **−0.58** | **−0.60** | **−0.49** | **0.68** | **−0.51** | −0.42 | −0.49 | **0.54** | **−0.59** | **0.54** | **0.61** | −0.28 | 1 | |
| LT | **−0.82** | **−0.76** | **−0.73** | **−0.78** | 0.42 | **0.93** | **0.76** | **0.66** | 0.72 | **0.81** | **0.76** | **−0.74** | **−0.71** | **−0.43** | **0.60** | 1 |
| TC | **−0.83** | **−0.84** | **−0.72** | **−0.72** | **0.58** | **0.67** | **0.76** | 0.57 | 0.68 | **0.81** | **0.92** | **−0.81** | **−0.85** | **−0.52** | −0.43 | **0.67** |

[a] Abbreviations for ground-flora groups are as follows: VAC = *Vaccinium*, ARU = *Arundinaria*, KAL = *Kalmia*, SMI = *Smilax*, VIT = *Vitis*, THE = *Thelypteris*, POL = *Polystichum*, SAN = *Sanguinaria*, ADI = *Adiantum*, TIA = *Tiarella*, RHO = *Rhododendron*. Abbreviations for tree groups are as follows: QC = *Quercus coccinea*, OA = *Oxydendrum arboreum*, QP = *Quercus prinus*, QA = *Quercus alba*, LT = *Liriodendron tulipifera*, TC = *Tsuga canadensis*.

most positively associated with the mesic *Tiarella* group determined by the Mantel test, for example, the xeric *Vaccinium* group was negatively associated with the *Tiarella* group in canonical correlation analyses. Related groups such as the mesic *Polystichum* and *Rhododendron* groups were positively associated, but negatively associated with xeric groups such as the *Vaccinium* and *Arundinaria* groups. Even the widespread *Smilax* group was positively associated with xeric groups and negatively associated with mesic groups, reflecting the subtle greater quantitative importance of the *Smilax* group in xeric ecosystems. Establishing association of the *Sanguinaria* and *Adiantum* groups with other groups was difficult because of the limited distribution and many zeros (absences) of these groups.

The *Quercus coccinea* and *Oxydendrum arboreum* tree groups were most positively associated with the *Vaccinium*, *Arundinaria*, *Kalmia*, and *Smilax* ground-flora groups, and were negatively associated with mesic groups such as the *Tiarella* group (Table 4). In contrast, the *Tsuga canadensis* tree group was most positively associated with the *Rhododendron* ground-flora group and most negatively associated with the xeric *Vaccinium* and *Arundinaria* groups. Likewise, several tree species groups were positively or negatively associated with other tree groups. The *Quercus coccinea* group, for example, cooccurred with the *Oxydendrum arboreum* group but was negatively associated with the *Tsuga canadensis* group. Canonical correlation was useful for identifying assemblages of ground-flora and tree groups that varied together across the landscape.

SPECIES GROUPS AND DISTURBANCE REGIMES. While species groups have been developed for a mix of late- and early successional forests (Archambault et al. 1989, Meilleur et al. 1992), little attention has been given to how the environmental relationships and composition of species groups may change in older forests in the absence of disturbance. Appalachian *Quercus* forests, for example, generally experienced reductions of historic fire frequencies through the 1900s (Brose et al. 2001). An absence of fire is expected to continue in many *Quercus* forests, and this may result in changes in the xeric *Vaccinium*, *Kalmia*, *Q. coccinea*, and other species groups classified in this study associated with *Quercus* forests. During this changing disturbance regime, *Pinus strobus* L., for example, has expanded its distribution from mesic sites to xeric *Quercus* sites in southern Appalachian forests (Abella and Shelburne 2003). While *P. strobus* was classified into a mesic species group in this study, *P. strobus* might be more appropriately classified into one of the xeric species groups in 20–30 years if the distribution and site relationships of this species continue to shift. Likewise, species of the *Vaccinium* group normally associated with open, fire-prone sites might exhibit a more restricted distribution confined to the most xeric sites of the landscape. While numerous authors have stressed that species groups developed on a study area should not be extrapolated far geographically because of variations in species-site relationships within a region (Pregitzer and Barnes 1982, Kashian et al. 2003), attention should also focus on how long species groups remain temporally robust during successional changes in undisturbed forests.

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