

Species Diversity and Composition in Old Growth and Second Growth Rich Coves of the Southern Appalachian Mountains

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ABSTRACT Because of ongoing debate over the long term impacts of logging, we conducted a study to assess if second growth (70 ± 10 years) rich coves differ from old growth rich coves (> 125 years) in species diversity or composition. We sampled twenty-six 0.1 ha plots, representing these two age classes. We distributed the plots amongst three randomly selected mountain ranges in the southern Appalachians of North Carolina, and sampled each mountain range in separate years. We used nested subplots of 0.01 m², 0.1 m², 1 m², 10 m², 100 m², and 1000 m² to establish species-area relationships (SARs) for each age class. We found no significant differences between the SARs for the two age classes, nor did we find significant differences between age classes using the Simpson, Shannon-Wiener, or Sorensen indices of species diversity. However, we found that total cover of all plant species was greater in old growth rich coves, and that 10% of the tested species had lower abundance in second growth. No species were present in old growth and absent in second growth, but species with lower second growth abundance may warrant future study.

INTRODUCTION Many ecologists have noted the diversity and grandeur of the southern Appalachian rich coves (Braun 1950, Whittaker 1956, Schafale and Weakley 1990, Ulrey 2002). Rich coves occur in mesic conditions with high soil fertility, and are located on mid to lower slopes, particularly along stream drainages. The virtual absence of a shrub layer combined with a lush herbaceous layer form a visually inviting community. The complex terrain, relative stability during the ice ages, and nutrient enrichment from upslope have all contributed to the evolution of a highly productive, species rich community, with numerous niche specialists and endemic plants (Whittaker 1956, Harden and Cooper 1967, Pittillo et al. 1998, Wen 1999).

Ulrey's (2002) research in the southern Appalachian region determined that rich

coves have wide distribution and high species richness. Braun (1950) established that rich coves differ substantially from one location to another. Of different vegetative strata in rich coves (tree, shrub, herb), the herb layer likely has the greatest variability (Braun 1950, Schafale and Weakley 1990), and may have the greatest sensitivity to disturbance (Duffey and Meier 1992, Gilliam 2002).

A number of studies have examined species composition differences between age classes within the mixed mesophytic forest of the southern Appalachians. Greenlee (1974) suggested that an old growth rich cove (> 300 years old) of Joyce Kilmer, North Carolina, and a neighboring second growth rich cove (age 16), differed in species composition but not in 1 m² species richness. However, a similar study by Meier et al. (1995) suggested differences in both species composition and richness. Furthermore, Meier et al. (1995) proposed several important theories regarding the mechanisms by which

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major disturbance, and especially logging, may cause decreased species richness in second growth rich cove forests. Unfortunately, neither of these studies had statistical replication necessary for more conclusive findings. A synthesis of several studies of rich mesic southern Appalachian forests (Greenlee 1974, Elliott et al. 1997, Ford et al. 2000, Gilliam 2002 and Jackson 2006), suggests that species diversity drops in years immediately after logging (Elliott et al. 1997), but that it subsequently recovers. Presumably, this dip in species diversity corresponds with canopy closure approximately 15 – 20 years after logging. Ford et al. (2000) found that 25 year old second growth coves did not significantly differ in species richness or diversity from ≥ 85 year old second growth coves. However, these studies do not clarify if older second growth stands have the same species richness or composition as old growth stands. Only Duffey and Meier (1992) directly addressed this more specific question, by examining richness at the 1 m² scale.

Duffey and Meier (1992) found that second growth rich cove forests (age 45 to 87 years) had significantly reduced herbaceous species richness at the 1 m² scale, compared to old growth rich coves. Duffey and Meier (1992) inferred that reduced species richness at 1 m² threatens individual species survival. However, many ecologists have called for additional research to better evaluate the potential long term impacts of disturbance on the rich cove community and its component species (Elliott and Loftis 1993, Johnson et al. 1993).

The studies to date have left questions regarding how second growth forest compares to old growth forest. Duffey and Meier's (1992) study generated questions about completeness because they: subjectively paired study sites, sampled at only one spatial scale, did not report on any individual species, and avoided areas of ericaceous shrubs. Studies by Greenlee (1974), Meier et al. (1995), and Jackson (2006) all lack statistical replication, while studies by Elliott et al. (1997), Ford et al. (2000) and Gilliam (2002) used second growth sites (54–77 years, 85+ years and 70+ years, respectively) as their control. Following the works of these prior studies, we established two objectives for quantifying species richness and composition in old growth (> 125 years old) and second growth (70 \pm 10 years):

- (1) Identify which spatial scales, if any, exhibit differences in species richness (Elliott and Loftis 1993).
- (2) Determine if any species have reduced abundance (percentage cover) in second growth (70 \pm 10 years) rich coves.

METHODS

Site Selection

Because of temporal constraints and the scarcity of old growth, researchers cannot practically use experimental methods for determining if second growth (70 years old) stands have the same species richness and composition as pre-disturbance (i.e. old growth) stands. Observational chronosequence studies offer the only feasible means to address this problem. However, site selections for chronosequence studies are challenging and controversial. Researchers must find objective means to equate sites for comparison, or risk invalidating results. Chronosequence studies ignore potential effects from environmental differences between age classes. Changes in climate, CO₂ levels, nutrient deposition, or anthropogenic influences such as logging methods, offer potential complications to assessments based on chronosequence studies. Still, chronosequence can offer great insight into successional pathways (Halpern 1988).

To objectively select field sites, we used a computer model of the Southern Appalachian Ecological Zones (SAEZ) (Simon et al. 2006) along with stand ages from the Continuous Inventory of Stand Conditions (CISC) database. We merged these data in ARC-GIS (© 2005, ESRI), and identified potential rich cove stands in two age classes (> 125 years old and 60–80 years old). We then identified three research blocks on United States Forest Service lands in North Carolina: the Unicoi, Nantahala, and Black/Craggy Mountain Ranges. We chose these based on uniform geology within blocks. We sampled these blocks in 2003, 2005, and 2006, respectively. Within each research block we chose four or five study plots per age class.

We accepted or rejected candidate sites based on two categories, accuracy of stand age (CISC records), and accuracy of the community type (SAEZ prediction). Recorded ages for second growth were generally based on logging records when entered into CISC; however, when in doubt, we cored one or two dominant trees to validate stand age. We

required that old growth sites meet the preponderance of recognized mixed-mesophytic old growth criteria (Greenberg et al. 1997, Hardt and Swank 1997, McCarthey 2003), to include:

- Stand density: 322 ± 85 trees per hectare (trees defined as ≥ 10 cm d.b.h.),
- Stand basal area: 38 ± 11 m²/ha,
- Maximum tree d.b.h.: 100 to 200 cm (dependent on species),
- Standing snags: 31 ± 19 snags per hectare,
- Large woody debris (downed logs): 155 ± 113 m³/ha,
- Decadent trees: 12 ± 6 aging trees in decline or decay per hectare (approximately 3% of living trees),
- Canopy gaps: $\sim 10\%$ of stand area in canopy gaps/decade, and
- No visual signs of previous logging (saw marks on stumps, proximity of logging roads, large number of "double" and "triple" stump sprouts in the canopy).

Of the 13 old growth sites chosen for this study, 7 were in areas of well documented "virgin" forest, with trees estimated in excess of 300 years old. Strict adherence to the above criterion led us to assess that the remaining 6 sites likely represented true "virgin" forest fragments, and not simply older second growth forest.

We assessed the plant community classification in a similar manner to the age, in order to verify that the SAEZ model of environmental traits actually support a rich cove community. We primarily used Ulrey's (2002) quantitative species lists by community, but we also referred to rich cove species identified by other authors (Braun 1950, Whittaker 1956, Radford et al. 1968, Schafale and Weakley 1990, Newell et al. 1997, Weakley 2008). We evaluated which community type each site most closely resembled (rich cove or otherwise). Valid rich cove sites met the preponderance of these criteria:

- $\geq 75\%$ canopy coverage of rich cove tree species (see Ulrey 2002 for listing of 21 potential rich cove tree species),
- $\leq 25\%$ *Tsuga canadensis* canopy coverage,
- $\leq 10\%$ shrub layer coverage of ericaceous shrubs (*Rhododendron* spp. and *Kalmia latifolia*),
- \leq modest presence of indicator species from other major community types (indicators defined by Ulrey 2002), and

- Dominant species acknowledged to grow in mesophytic conditions.

Due to errors in the SAEZ model and CISC databases, we needed to validate each nominated site. We visited 62 nominated sites in an effort to meet our desired goal of 30 sites (15 in each age class). Despite our extensive field search, we were only able to objectively identify 13 old growth rich cove sites within our 3 study blocks. Correspondingly, we sampled 26 plots (experimental units), with 13 in each age class. Of the other 36 candidate sites we rejected, half had inaccurate age classification from the CISC database and half had inaccurate community prediction from the SAEZ model. We desired a larger sample size for statistical purposes, but were constrained by scarcity of valid old growth sites, time and funding.

Ulrey (2002) found rich coves occurring between 550 m–1430 m (1850 ft to 4700 ft), however we only sampled rich coves between 825 m–1430 m (2600 ft to 4700 ft). Twenty-three of the twenty-six sites occurred between 1070 m–1370 m (3500 ft–4500 ft). We did not intentionally constrain the sample population, but we only found old growth rich coves at higher elevations in our three sample blocks. We presume these higher elevation sites were less accessible during the widespread logging of the late 1800's and early 1900's. Sample sites tended toward northeasterly aspects, ranging from 330° to 115°. Site slopes ranged from 15° to 39°.

Field Sampling

We established each plot (experimental unit) following the Carolina Vegetation Survey (CVS) methodology (Peet et al. 1998). This methodology uses a 20 m by 50 m plot layout, with 8 nested subplots (Figure 1). Because of the limited number of old growth sites, we increased the number of subplots (sample units) per plot in order to moderately increase statistical power. We placed additional subplots in the corners of unused modules (100 m² subplots). Placement of the additional subplots was chosen as part of a separate study to investigate the difference in nested versus non-nested subplots.

We sampled each block from the second week of May through the second week of June, in an effort to minimize seasonal variability of abundances. We recorded the presence of

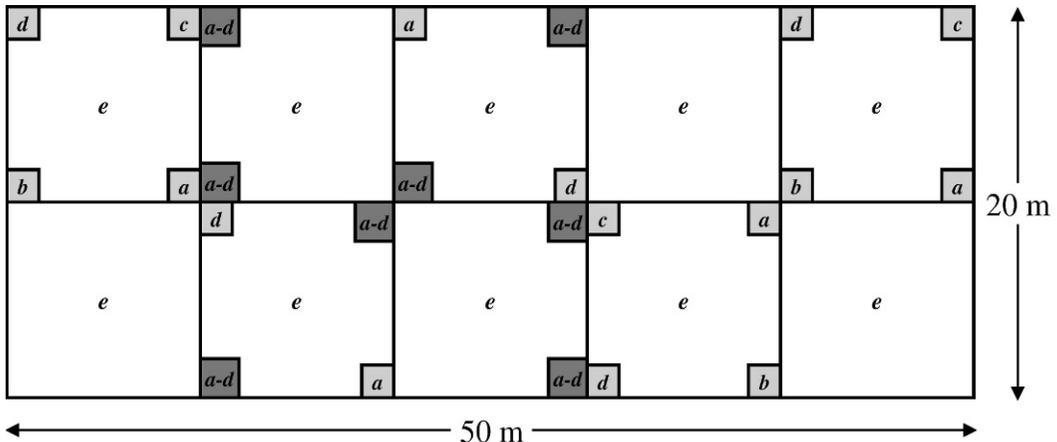


Figure 1. Modified Carolina Vegetation Survey plot design.

- Whole Plot: 1000 m² (20 m by 50 m)
- Subplots: $a = 0.01 \text{ m}^2$, $b = 0.1 \text{ m}^2$, $c = 1 \text{ m}^2$, $d = 10 \text{ m}^2$, $e = 100 \text{ m}^2$
- $a-d$ = nested subplots of scales 0.01 m² through 10 m²
- Adapted from Peet et al. (1998).

all species rooted in each plot or subplot. For the 100 m² subplots, we recorded the percentage cover (abundance) of each species. Species concepts and nomenclature follow Weakley (2008).

When establishing each plot, we searched to find the most prominent local drainage within the predicted rich cove, usually an ephemeral or 1st order stream. We then placed the plot to straddle the stream, with the 50 m length of the plot running parallel to the slope contour. We established the plot at the most concave portion of the slope, which seemed the most consistent topographic position for rich coves.

Analysis of Species Diversity (Objective 1)

To test for age differences in species richness (Objective 1), we calculated the mean number of species (richness) for the six spatial scales in each plot (0.01 m², 0.1 m², 1 m², 10 m², 100 m², and 1000 m²). Our statistical hypotheses were:

H_0 : Species:Area curves for second growth rich coves = Species:Area curves for old growth rich coves ($\alpha = .05$, Power = .91) [Power calculations from Lenth (2006)]

H_a : Species:Area curves for second growth rich coves \neq Species:Area curves for old growth rich coves ($\alpha = .05$, Power = .91)

We modeled the species-area relationship for both the old growth and second growth

age classes using the power model (Log10 transformations of both the species count and the spatial scale; Arrhenius 1921, He and Legendre 1996, Fridley et al. 2005). Due to the explicit structure of these spatial data, we used a repeated measures analysis to assess the species-area relationship (SAR; Whittaker 1972, Swallow 1984, McCune and Grace 2002) using SAS[®] software version 9.1.3. To facilitate comparison with previous studies that included species richness for single spatial scales, we also conducted a separate ANOVA for each spatial scale. For comparison with Duffey and Meier's (1992) study of herbs, we also calculated herbaceous richness (excluding trees or shrubs species) at the 1 m² scale.

In addition to determining the species richness and SAR, we calculated the Simpson and Shannon-Weiner indices for diversity, as well as the Sorensen similarity index, following methods summarized in McCune and Grace (2002). For both the old growth and second growth, we calculated diversity by the Simpson's diversity index (Equation (1.1)), where P_i is the proportion of total abundance belonging to species i , and the Shannon-Wiener index (Equation (1.2)). To evaluate the similarity of second growth to old growth rich coves, we calculated the Sorensen index, (Equation (1.3) where w is the shared abundance by species in each age class, while A and B are the total abundance in each age class).

$$1 - \sum P_i^2 \quad (1.1)$$

$$H' = - \sum (P_i * \log P_i) \quad (1.2)$$

$$2w/(A + B) \quad (1.3)$$

Analysis of Species Composition (Objective 2)

To test for age differences in species composition (Objective 2), we calculated the mean abundance (percentage cover) for all species at each 100 m² subplot. We present a multivariate community analysis in rich coves elsewhere (Jackson et al. 2008). Our statistical hypotheses were:

H₀: Abundance in second growth rich coves ≥ abundance in old growth rich coves (α = .10, Power = .96)

H_a: Abundance in second growth rich coves < abundance in old growth rich coves (α = .10, Power = .96)

Following Platt's (1964) strong inference model, we crafted our hypotheses and analytical methods to address the most important question: "Which species have risk of local extirpation or extinction due to disturbance?" We examined the consequence of both Type I and Type II errors for the t-tests of differences in abundance. Type I errors (erroneously reject H₀) protect non-threatened species, while Type II errors (erroneously fail to reject H₀) overlook threatened species. Therefore, we placed greater importance on minimizing Type II error (increasing statistical power) over Type I error. For these reasons, we:

- Used α = .10 to test age differences for individual species,
- Conducted a 1-tailed t-test (instead of a 2-tailed) to focus the statistical power on only those species at risk (species with greater old growth abundance),
- Utilized the Least Significant Difference (LSD) Multiple Comparison Procedure (MCP) which favors increased power over moderating Type I error.

We followed the Carolina Vegetation Survey inventory methodology (Peet et al. 1998) and estimated the percentage cover of each species at the 100 m² scale. In contrast with the CVS protocol, we subsampled all ten 100 m² subplots per plot, instead of only four

100 m² subplots. Next, we conducted a 1-tailed t-test of the null hypothesis (H₀: second growth abundance ≥ old growth abundance) versus the alternative hypothesis (H_a: second growth abundance < old growth abundance), using SAS® software v. 9.1.3. The 1-tailed t-test focuses statistical power on species with greater old growth abundance, but precludes assessment of species with greater second growth abundance. However, when we checked the variance heterogeneity, we found a strong wedge-shape in the plot of the variances. Therefore, we tested arc-sine transformations of the abundance data (Steele et al. 1997), which resulted in a more appropriate "cloud shaped" variance distribution.

We generated a table of the most common rich cove species, where the number of species in the list equaled the mean species richness at the 1000 m² scale (79 species). We determined the mean number of species for trees (15), shrubs (2) and herbs (62) per plot, and identified the most abundant species in each growth form for inclusion in this "constancy table" of common rich cove species. In addition to testing for differences in abundance for each individual species, we conducted a t-test for differences in the total percentage cover (abundance) of all plant species by age class.

In evaluating individual species in our constancy table, we were faced with a statistical dilemma: testing of 79 species constitutes a Multiple Comparison Procedure (MCP). MCPs are intended for applications where the number of experimental degrees of freedom exceeds the number of comparisons; however, our experiment had 25 degrees of freedom and 79 comparisons. We acknowledge this statistical shortcoming, but we contend that it is better to evaluate more species with some errors than fewer species with more limited errors. In line with this position, we listed the t-test results (H₀: second growth abundance ≥ old growth abundance) for all 79 of the most abundant species, and rank ordered the constancy table based on the p-values. Because of our liberal usage of MCPs, our results should be viewed as exploratory, with a bias towards identifying species with lower 2nd growth abundances.

RESULTS

Species Diversity (Objective 1)

The two age classes did not differ in their species-area relationships (F < 0.01, p-value

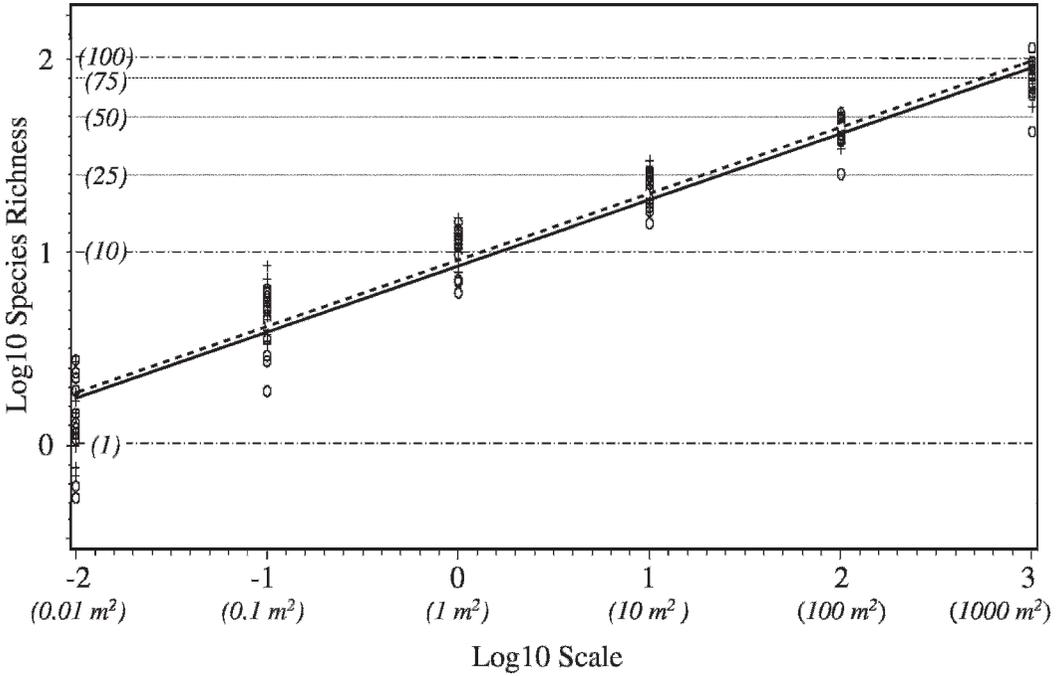


Figure 2. Species-area relationships for second growth (age 70 ± 10 years) and old growth (age > 125 years) rich coves.

- Regression Equations:

Old Growth: $Y(\text{Log}_{10} \text{ species count}) = 0.929384 + 0.341975 (\text{Log}_{10} \text{ Scale})$	Regression: _____	Plot: ○
2 nd Growth: $Y(\text{Log}_{10} \text{ species count}) = 0.956811 + 0.343812 (\text{Log}_{10} \text{ Scale})$	+
- (“o” = old growth and “+” = second growth plot means).
- Secondary axis labels in parenthesis represent the original, non-transformed values.
- 95% Confidence Bands for regression lines showed no difference between age classes; bands have been omitted for clarity.

= 0.97) (Figure 2). Congruent with these results, none of the individual scales showed differences in richness (Table 1). We failed to reject H_0 and concluded that second growth (age 70 ± 10 years) rich cove species richness was equivalent to old growth (age > 125 years) species richness across all measured scales (0.01 m^2 to 1000 m^2).

Next, we compared our findings of herbaceous species with those of Duffey and Meier (1992). We found 9.3 herbaceous species/ m^2

in old growth and 9.8 species/ m^2 in second growth, with no significant difference between ages ($p = 0.57$). Duffey and Meier found 10.9 herbaceous species per m^2 in old growth and 6.6 per m^2 in second growth, where all 9 study locations had significantly greater old growth richness (all p values < 0.05).

We found approximately 5 species/ 0.1 m^2 , 10 species/ 1 m^2 , 20 species/ 10 m^2 , 40 species/ 100 m^2 , and 80 species/ 1000 m^2 (Table 1).

Table 1. Species richness comparison by scale, between second growth (age 70 ± 10 years) and old growth (age > 125 years) rich coves

Scale (m^2)	Old Growth Species Richness	2nd Growth Species Richness	Standard Error	F-test of Age Difference Pr > F
0.01	1.5	1.5	0.18	0.95
0.1	4.7	4.9	0.51	0.76
1	10.5	11.3	0.65	0.50
10	21.3	23.6	1.19	0.28
100	42.0	45.9	2.05	0.25
1000	78.5	78.6	4.38	0.98

Interestingly, our results closely follow the species-area relationship summarized by MacArthur and Wilson (1967), where a 10 fold increase in area resulted in a doubling of species richness.

We conducted species diversity measures at the 0.1 ha scale, based on the mean percentage cover per species by age class. Old growth rich coves had a Simpson index [Equation (1.1)] of 0.957 and a Shannon-Wiener index [Equation (1.2)] of 1.68, while second growth rich coves had results of 0.969 and 1.91 respectively. Furthermore, the Sorensen index [Equation (1.3)] resulted in 0.75. Barbour et al. (1999) indicate that Sorensen index of ≥ 0.50 represents the same association. But, we noted that this Sorensen comparison did not account for the confidence intervals on each species in each age class. Therefore, we recalculated the Sorensen based on 90% confidence intervals of abundance by species by age class. The subsequent Sorensen index showed 0.95 similarity between the old growth and second growth.

Species Composition (Objective 2)

We encountered 378 taxa amongst the 26 plots, with an average of 79 species per 0.1 ha plot. Our constancy table of the most abundant species by growth form included 62 herb, 2 shrub, and 15 tree species (Table 2). All 79 common species were present in both age classes. Of the 79 constancy species, eight had significantly greater abundance in old growth ($p \leq 0.10$).

Old growth rich coves had significantly greater percentage coverage from all species than did the 70 year old coves ($F = 4.54$, $p = 0.04$). Second growth rich coves averaged 168% cover from all plant species, while old growth rich coves averaged 197% cover.

DISCUSSION

Species Diversity (Objective 1)

We found no difference in species richness, species diversity (Simpson, Shannon-Wiener), or in Sorensen's similarity index, between the old growth and second growth rich coves. Furthermore, the Species Area relationship (SAR) was virtually identical between the two age classes. Our herbaceous species richness results contrast with Duffey and Meier's (1992) findings at the 1 m² scale. Based on 95% confidence intervals from each of our studies, our old growth species richness was

significantly lower than Duffey and Meier's study, but our second growth species richness was significantly greater than in Duffey and Meier's study. Possible causes for these differences include:

- (1) Differences in site selection. Duffey and Meier used subjective site selection which may have introduced bias, while we used random site selection based on computer modeling that was not previously available.
- (2) Differences in sampling methodology: Duffey and Meier employed randomized sampling, but notably avoided areas with *Rhododendron* spp. We sampled with systematically placed subplots.
- (3) Variability in weather effects. Duffey and Meier sampled in only one growing season, while we sampled over 3 growing seasons. Random climatic effects may have contributed to the differences in species counts.

Species Composition (Objective 2)

Although we found no differences in species diversity or the SAR, we found compositional differences between old growth and second growth rich coves. Eight species had significantly less abundance ($\alpha = .10$) in second growth (70 \pm 10 years) compared to old growth (> 125 years) rich coves. These differences are similar to findings from other studies (Greenlee 1974, Elliott et al. 1997, Ford et al. 2000). However, these authors encountered some early successional species which were absent in both of our age classes (*Potentilla canadensis* L., *Erechtites hieracifolia* (L.) Rafinesque ex Augustine de Candolle, *Acalypha rhomboidea* Rafinesque, *Panicum* spp., among others). By age 70, successional processes apparently resulted in the loss of these disturbance-related species.

Twenty-nine percent (4 of 14) of the Ulrey's (2002) rich cove indicator species had significantly lower second growth abundance ($\alpha = .10$), compared to only ten percent (8 of 79) of the total number of species tested. We hypothesized that the indicator species were more likely to have lower second growth abundance than were the non-indicator species. We tested this with a simple Wilcoxon rank-sum test, using the p-values of abundance differences for indicators versus non-indicator species. This test showed that the

Table 2. Rich cove constancy table: 79 most abundant species (62 herb, 2 shrub, and 15 tree) sorted by 1-tailed t-test of cover in old growth (age > 125 years) > second growth (age 70 ± 10 years)

Species	Old Growth Mean Cover	2nd Growth Mean Cover	Old Growth Frequency of Occurrence	2nd Growth Frequency of Occurrence	P value
<i>Anemone quinquefolia</i> Linnaeus	0.56	0.20	1.00	0.69	0.01
<i>Diphylleia cymosa</i> Michaux	0.55	0.20	0.62	0.46	0.04
* <i>Laportea canadensis</i> (L.) Weddell	10.97	3.14	0.85	0.85	0.05
<i>Thelypteris noveboracensis</i> (L.) Nieuwland	1.07	0.19	0.54	0.31	0.07
<i>Athyrium asplenoides</i> (Michaux) A.A. Eaton	1.51	0.17	0.69	0.46	0.08
* <i>Fraxinus americana</i> Linnaeus	7.94	3.29	0.85	0.69	0.09
* <i>Galium triflorum</i> Michaux	0.35	0.25	0.92	0.69	0.10
* <i>Trillium erectum</i> Linnaeus	0.48	0.41	1.00	1.00	0.10
<i>Actaea podocarpa</i> A.P. de Candolle	3.12	1.00	0.69	0.69	0.11
* <i>Aesculus flava</i> Solander	15.06	8.33	0.92	0.92	0.14
* <i>Prosartes lanuginosa</i> (Michaux) D. Don	1.10	0.78	0.92	1.00	0.14
* <i>Actaea racemosa</i> Linnaeus	1.66	0.90	0.54	0.38	0.14
<i>Stellaria pubera</i> Michaux	0.66	0.38	0.77	0.69	0.16
<i>Carex pennsylvanica</i> Lamarck	0.20	0.14	0.31	0.38	0.17
<i>Fagus grandifolia</i> Ehrhart	7.84	4.55	0.69	0.62	0.18
<i>Impatiens</i> cf. <i>capensis</i> Meerburg	0.55	0.18	0.69	0.69	0.18
* <i>Caulophyllum thalictroides</i> (L.) Michaux	2.66	1.49	1.00	1.00	0.19
<i>Prenanthes</i> spp.	0.50	0.36	0.92	0.92	0.20
<i>Poa compressa</i> Linnaeus	0.13	0.11	0.62	0.23	0.21
<i>Halesia tetraptera</i> Ellis	4.94	2.54	0.46	0.38	0.21
<i>Dioscorea quaternata</i> J.F. Gmelin	0.25	0.21	0.77	0.62	0.22
<i>Ageratina altissima</i> King and H.E. Robinson	0.25	0.14	0.77	0.38	0.23
<i>Hydrophyllum canadense</i> Linnaeus	0.40	0.28	0.77	0.69	0.23
<i>Podophyllum peltatum</i> Linnaeus	1.78	0.29	0.54	0.54	0.26
<i>Smilax herbacea</i> Linnaeus	0.14	0.14	0.69	0.46	0.27
<i>Medeola virginiana</i> Linnaeus	0.25	0.16	0.62	0.62	0.27
* <i>Tilia americana</i> Linnaeus	16.08	13.26	1.00	0.92	0.28
<i>Polygonatum pubescens</i> (Willdenow) Pursh	0.25	0.22	0.85	0.69	0.31
<i>Collinsonia canadensis</i> Linnaeus	0.57	0.38	0.85	0.77	0.32
<i>Panax quinquefolius</i> Linnaeus	0.10	0.06	0.54	0.62	0.32
<i>Viola pubescens</i> Aiton	0.28	0.19	0.54	0.62	0.32
* <i>Osmorhiza claytonii</i> (Michaux) C.B. Clarke	0.45	0.32	0.77	0.77	0.33
<i>Uvularia perfoliata</i> Linnaeus	0.10	0.08	0.46	0.38	0.36
<i>Viola rotundifolia</i> Michaux	0.34	0.26	0.69	0.77	0.38
<i>Viola sororia</i> Willdenow	0.29	0.22	0.54	0.54	0.39
<i>Betula alleghaniensis</i> Britton	13.42	11.78	0.77	0.69	0.40
<i>Polystichum acrostichoides</i> (Michaux) Schott	1.91	1.81	1.00	1.00	0.41
<i>Dicentra canadensis</i> (Goldie) Walpers	0.30	0.23	0.38	0.38	0.41
<i>Eurybia chlorolepis</i> (Burgess) Nesom	1.86	1.38	1.00	1.00	0.41
<i>Smilax rotundifolia</i> Linnaeus	0.06	0.09	0.54	0.31	0.45
<i>Dryopteris intermedia</i> (Muhl. ex Willd.) A. Gray	1.25	1.14	0.85	0.92	0.46
<i>Tiarella cordifolia</i> Linnaeus	0.54	0.43	0.69	0.77	0.47
* <i>Acer saccharum</i> Marshall	33.28	27.53	0.92	1.00	0.49
<i>Rubus canadensis</i> Linnaeus	0.18	0.22	0.62	0.54	0.49
<i>Dryopteris marginalis</i> (Linnaeus) A. Gray	0.63	0.51	0.62	0.69	0.50
<i>Viola hastata</i> Michaux	0.19	0.17	0.62	0.69	0.52
<i>Cornus alternifolia</i> Linnaeus	0.17	0.13	0.54	0.62	0.52
<i>Clintonia umbellulata</i> (Michaux) Morong	0.12	0.13	0.46	0.54	0.54
<i>Acer rubrum</i> Linnaeus	2.20	2.55	0.46	0.54	0.55
<i>Cardamine diphylla</i> (Michaux) A. Wood	0.57	0.65	0.85	0.85	0.57
<i>Anemone acutiloba</i> A.P. de Candolle	0.41	0.61	0.15	0.23	0.58
* <i>Viola canadensis</i> Linnaeus	2.49	2.41	0.62	0.62	0.59
<i>Cardamine concatenata</i> (Michaux) Schwarz	0.16	0.37	0.46	0.38	0.60
<i>Deparia acrostichoides</i> (Swartz) M.Kato	1.09	1.94	0.62	0.46	0.61
<i>Solidago</i> c.f. <i>caesia</i> Linnaeus	0.96	0.99	0.92	1.00	0.62
<i>Trillium grandiflorum</i> (Michaux) Salisbury	0.17	0.25	0.69	0.54	0.64
<i>Acer pensylvanicum</i> Linnaeus	4.64	8.57	0.85	0.92	0.66
<i>Veratrum parviflorum</i> Michaux	0.63	0.69	0.69	0.77	0.67
<i>Galium latifolium</i> Michaux	0.10	0.22	0.62	0.46	0.68

Table 2. Continued

Species	Old Growth Mean Cover	2nd Growth Mean Cover	Old Growth Frequency of Occurrence	2nd Growth Frequency of Occurrence	P value
<i>Botrypus virginianus</i> (Linnaeus) Holub	0.18	0.23	0.69	0.69	0.69
<i>Liriodendron tulipifera</i> Linnaeus	2.37	6.54	0.23	0.46	0.70
<i>Polygonatum biflorum</i> (Walter) Elliott	0.26	0.27	0.85	0.92	0.70
<i>Actaea pachypoda</i> Elliott	0.31	0.89	0.77	0.77	0.72
<i>Thalictrum dioicum</i> Linnaeus	0.22	0.25	0.38	0.62	0.74
<i>Arisaema triphyllum</i> (Linnaeus) Schott	0.37	0.43	0.85	0.92	0.75
<i>Stellaria corei</i> Shinnars	0.32	1.01	0.15	0.23	0.75
<i>Magnolia acuminata</i> (Linnaeus) Linnaeus	0.38	0.79	0.62	0.62	0.76
<i>Prunus serotina</i> Ehrhart	2.62	4.79	0.85	1.00	0.76
<i>Maianthemum racemosum</i> (Linnaeus) Link	0.22	1.69	0.85	0.92	0.83
<i>Tsuga canadensis</i> (Linnaeus) Carriere	1.40	2.55	0.38	0.46	0.84
<i>Astilbe biternata</i> (Ventenat) Britton	0.46	1.53	0.46	0.54	0.88
<i>Lilium superbum</i> Linnaeus	0.11	0.18	0.54	0.69	0.89
<i>Quercus rubra</i> Linnaeus	3.93	6.07	0.85	0.85	0.90
* <i>Sanguinaria canadensis</i> Linnaeus	0.12	0.27	0.46	0.69	0.90
<i>Uvularia grandiflora</i> J.E. Smith	0.24	0.17	0.38	0.54	0.91
<i>Ribes cynosbati</i> Linnaeus	0.12	1.07	0.23	0.46	0.92
<i>Betula lenta</i> Linnaeus	3.49	3.78	0.46	0.54	0.94
* <i>Hydrangea arborescens</i> Linnaeus	0.29	0.99	0.62	0.92	0.95
<i>Isotrema macrophylla</i> (Lamarck) C.F. Reed	0.20	3.39	0.38	0.77	0.98

Frequency of Occurrence = number of plots of occurrence \div 13 (total number of plots by age class).

*= Rich cove indicator species identified by Ulrey (2002).

All data collected from the Unicoi, Nantahala, Black and Craggy Mountains, North Carolina.

indicator species had stronger age related differences than did the non-indicators ($p = 0.01$), and provides support to our theory that indicator species tend toward lower second growth abundance.

By definition, indicator species have high constancy and fidelity within a community. All 79 species in Table 2 meet the first part of this definition. In contrast, Ulrey's (2002) 14 rich cove indicator species have high fidelity to the rich cove community. These indicator species are niche specialists, while the non-indicator species have broader ecological amplitude. Based on this reasoning and our study results, we theorize that less common species which are endemic to rich coves may be at risk of lower second growth abundance. Conversely, generalist species are more plastic and appear better suited to higher second growth abundance.

Summary

Second growth (70 \pm 10 years) did not differ in species diversity or species-area relationship (SAR) from old growth (> 125 years) rich coves, although some species had reduced second growth abundance. Notably, all tested species were present to some degree in both age classes. Species with narrower ecological

amplitude (niche specialists) tended toward lower second growth abundances, while species with broader ecological amplitude (generalists) tended toward lower old growth abundances. These findings suggest that residual effects of logging are evident at age 70 \pm 10 years.

Duffey and Meier (1992) found lower second growth species diversity, and stated that "mixed mesophytic forests of the Appalachians appear unlikely to recover within the present planned logging cycles of 40–150 years, suggesting a future loss of diversity of understory herbaceous plants". By contrast, our study found no age related differences in the species-area relationship (SAR) in rich coves, refuting the need to extend rotation lengths for the sake of species richness. However, we found that 10% (8 out of 79) of the species had lower second growth abundances.

Having found some species with lower abundance in second growth rich coves, we recommend three potential options for further research to assess the implications of future logging. The first option entails observation of older aged second growth rich coves (> 80 years). This option entails substantial drawbacks because it will be expensive and

time consuming. Identification of stands logged prior to ~ 1925 becomes increasingly difficult to find and properly age due to inadequacies of older records. The second option establishes permanent plots to track changes over time for both old growth and second growth age classes. However this requires intensive study (and funding) over time, and may be impractical because of the slow return for results. The third option would focus on the improved understanding of the life history of species with lower second growth abundance. Having identified a short list of species, researchers can now investigate what mechanisms likely contribute to lower abundances. Meier et al. (1995) offered several good theories that researchers may begin to test. Factorial greenhouse trials with different levels of light, moisture, soil fertility, and temperature (designed to mimic differences between levels in different timber harvest methods), should offer considerable insight. Furthermore, careful field observation, time lapse photography, or video may provide understanding of pollinators and dissemination methods.

Ultimately, society and policy makers must determine what level of reduced abundance is acceptable and compatible with management objectives. Continued research into the age related differences of species composition should aid in future decision making and management.

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