

ABSTRACT

B. CLAY JACKSON. Vegetation Differences in Neighboring Old Growth and Second Growth Rich Coves in the Joyce Kilmer Wilderness Area: A Thirty-two-year Perspective. (Under the direction of H. Lee Allen).

*I surveyed vegetation in neighboring old growth and second growth rich coves in the Joyce Kilmer Wilderness Area, North Carolina. This data, combined with data from three previous studies, provide a 32 year perspective of stand structure, species frequencies of occurrence at the 1 m² scale, and species richness at the 1 m² scale. I sampled one 0.1 ha plot in each cove. I subdivided each plot into ten 10 m by 10 m modules and sampled percentage cover of all species present in each module, plus stem diameter for woody stems. Additionally, I sampled presence absence in a variety of subplots at scales of 0.01 m², 0.1 m², 1 m², 10 m², and 100 m². A cohort of 30-40 cm diameter at breast height *Liriodendron tulipifera* trees dominated the second growth cove, while the old growth site had a broader mix of species with an inverse J-shape diameter distribution. In both rich coves, the frequencies of occurrence at 1 m² appeared highly variable for individual species between sample years and distances of 200 m or less.*

The four studies provided species richness comparisons at the 1 m² scale between the old growth and second growth (at ages 16, 35, 39, and 47 years). I concluded that the differences in second growth species richness between studies demonstrated rich cove forest succession. High species richness following disturbance reflected a surge of opportunistic species (age 16). The opportunistic species declined following canopy closure, resulting in significantly lower species richness (age 35). After further stand development, a resurgence of late-succession species increased species richness to equal levels with old growth (age 39 and 47).

Finally, I examined species-area relationships between the two coves, and between these rich coves and the regional average. Arrhenius model (\log_{10} species: \log_{10} area between the scales of 0.1 m^2 to 1000 m^2) species-area curves indicated no difference in species-area relationships between the two coves. Collectively, these two rich coves had a significantly higher intercept but no difference in regression slope from the regional average. These findings reflect an average rate of species accumulation in the Joyce Kilmer coves, but with higher-than-average species density at all measured scales.

**VEGETATION DIFFERENCES IN NEIGHBORING OLD GROWTH AND SECOND
GROWTH RICH COVES IN THE JOYCE KILMER WILDERNESS AREA: A THIRTY-
TWO-YEAR PERSPECTIVE**

by

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I dedicate this work to my Grandpa,

William (Bill) Chadwick Hunnicutt,
(1919-2002)

At an early age, he taught me a genuine love and respect for nature.

BIOGRAPHY

B. Clay Jackson was born in Raleigh, North Carolina in 1971. He grew up in Raleigh and in Memphis, Tennessee. At age 14 he became an Eagle Scout in the Boy Scouts of America. Then at age 18, he was an exchange student in Åkersberga, Sweden.

From 1991 until 1996, Clay studied forestry at North Carolina State University (NCSU). While at NCSU, he was a teaching assistant at the Forestry Summer Camp (1994) and a member of the College of Forestry's student council (1995/6). Clay also became a Resident Advisor, a job which serendipitously introduced him to his future wife, Lari. He graduated *magna cum laudi* in 1996 with a B.S. in Forestry, a B.S. in Natural Resource Management, and a minor in International Relations. He also completed the College of Forestry's honor's program.

After graduating, Clay chose to serve his country and enlisted as an infantryman in the United States Army. Following an initial assignment at Ft. Benning, GA, Clay went on to attend Officer Candidate School and was commissioned as a 2nd Lieutenant. His later assignments included Seoul, South Korea (1998-1999) and Bad Kreuznach, Germany (1999-2001). In 2000, he was deployed to Kosovo, Yugoslavia, as part of the NATO Peacekeeping mission. Early the next year, Clay married Dr. Lari Meeker Jackson. Clay left the active duty Army in August 2001, to attend graduate school at NCSU. However, in August of 2003 he was recalled to active duty as a member of the 30th Brigade of the North Carolina National Guard. Clay and Lari's son, Aiden Grey Jackson, was born in March 2004, just days before Clay deployed to Diyala, Iraq with the 1st Infantry Division. For services in Iraq, he was awarded the Bronze Star. In July of 2005 Clay resumed his graduate studies at NCSU.

Currently, Clay, Lari and Aiden live in Raleigh NC. Together, they enjoy reading, traveling, exploring, games, back yard play, and (once exhaustion sets in) curling up on the couch. With Aiden's prompting, they stop often to smell the flowers.

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INTRODUCTION

Only a few studies have directly evaluated the conservation of species diversity in rich coves. Greenlee (1974) found no difference in species diversity between a 16 year-old regenerating rich cove and a neighboring old growth site, despite differences in species composition. In contrast, Duffey and Meier (1992) reported a significant reduction in species diversity among second growth rich coves compared to old growth rich coves. Both of these studies sampled and compared data from two specific rich coves in Joyce Kilmer Wilderness, North Carolina. The apparently conflicting results of these two studies provided the impetus for the current study.

The rich cove community type is part of the mixed mesophytic forest and has a lush, diverse herbaceous stratum (Braun 1950, Whittaker 1956, Schafale and Weakley 1990, Ulrey 2002). Both the public and scientific community show great interest in rich coves because of their inherent diversity and beauty. The rich cove community, also known as cove-hardwood community, is one of only four community types specified for monitoring in the Nantahala and Pisgah Land and Resource Management Plan (LMP) (USDA Forest Service 2005).

Systematic inventory of the southern Appalachian ecosystems did not begin until the latter half of the 1900's, after widespread logging had occurred. Because preharvest inventory data do not exist, we must rely on old growth forests to provide a baseline of biodiversity. The Nantahala, Pisgah, Chattahoochee, and Cherokee National Forests have 336,623 ha listed as "current old growth and potential future old growth", including 88,746 ha of mixed mesophytic forests (Table 1) (USDA Forest Service 1994, 2004a, and 2004b). However, the Nantahala and Pisgah LMP estimates that less than one-quarter of these potential old growth lands currently qualify as true old growth. Of these, the Joyce Kilmer-

Slickrock Wilderness Area is one of only three locations in North Carolina estimated to have over 2,500 ha of existing old growth (USDA Forest Service 1994, Appendix K).

Old growth rich coves are characterized by (1) complex vertical structure, (2) canopy mixed with shade-intolerant and shade-tolerant species, (3) multistructural herbaceous layer, (4) basal area averaging near carrying capacity at 40 m²/ha, (5) decadent trees, (6) standing snags, and (7) large woody debris (Greenberg et al. 1997, Hardt and Swank 1997). The complex vertical structure and mix of both shade tolerant and intolerant species in old growth forests represent ongoing gap-dynamic regeneration of mixed mesophytic climax forest (Runkle 1982, Clebsch and Busing 1989, Busing 1998, Runkle 1998). Under natural conditions, these uneven-aged climax forests produce gaps at a rate of 5 to 10% of the forest canopy per decade (Lorimer 1980, Runkle 1982).

The southern Appalachians generally have only modest fertility; however, coves tend to have higher nutrient status and soil moisture as catchments of throughflow from upslope (Pittillo et al. 1998). The combination of a moderate disturbance regime (gap dynamics) and moderate to high soil fertility provide conditions for high species richness relative to other community types (Tilman and Pacala 1993). Many authors have described changes in species richness during forest succession (see Horn 1974 for summary), and they have typically reported high species richness just after disturbance. Species richness typically declines during initial canopy closure, with a resurgence of late-succession species and species richness after further stand development.

Several authors suggest that the diverse herbaceous layer of cove forests is sensitive to harvest-related disturbance (Duffey and Meier 1992, Meier et al. 1995, Gilliam 2002). Opportunistic species increase in abundance, while late-succession species decline. Within

the rich cove community, it remains unclear which species may be at risk of permanent reduction or extirpation following disturbance. Understanding successional changes in each species' abundance and frequency of occurrence will help land managers identify sensitive species and remedy undesired impacts.

Following the work of three previous studies (Greenlee 1974, Duffey and Meier 1992, Newell et al. 1997), we sampled two similar and neighboring coves, one old growth and one second growth, in Joyce Kilmer – Slickrock Wilderness. Our primary objective was to synthesize these four studies in order to describe the two sites over a 32 year period. Because of differences in sample designs between studies, we focused on describing (1) stand structure, (2) species frequencies at the 1 m² scale, and (3) species richness at the 1 m² scale.

STUDY SITE

The Joyce Kilmer Wilderness lies within the Big Santeetlah Creek basin, just southwest of the Great Smoky Mountains National Park. The majestic trees and vibrant herbs of this primeval forest have fascinated ecologists for decades. Published works include descriptions of old growth forests (Braun 1950, Oosting and Bourdeau 1955, Tucker 1973, Lorimer 1980, Runkle 1982), comparisons between old growth and second growth cove vegetation (Greenlee 1974, Duffey and Meier 1992), and characterization of soils (Greenlee 1974, Daniels et al. 1987, Jones 2000). Newell et al. (1997) provided an in depth review of Joyce Kilmer Wilderness' history, ecology and vegetation. Furthermore, they established local community types based on multivariate analysis from their survey across the entire wilderness area. Many authors cite the undisturbed forest of Joyce Kilmer Wilderness as a

point of reference in defining regional vegetative communities and ecology types (Braun 1950, Schafale and Weakley 1990, Ulrey 2002, Simon et al. 2006).

Greenlee (1974) surveyed the rich coves in two neighboring watersheds within Joyce Kilmer Wilderness. Poplar Cove (old growth), lies near the mouth of the Little Santeetlah Creek basin and is well documented for its large yellow poplar (*Liriodendron tulipifera*) and hemlock (*Tsuga canadensis*) trees. Horse Cove (second growth) is a smaller cove, located in the watershed just east of Poplar Cove. Both sites are characterized by a north-northeast aspect at 850m elevation, and both are now part of the Joyce Kilmer – Slickrock Wilderness, in Graham County, North Carolina. Greenlee (1974) found that many species occurred in both coves but had greater abundance in one cove than in the other. Furthermore, he stated that herbaceous layer composition was the most obvious difference in the two coves.

METHODS

We took great care to embed our two study areas within those used by Greenlee (1974). Greenlee's thesis provided maps showing specifically where he had surveyed in each cove. We placed one 0.1 ha (20 m x 50 m) plot in the center of each of Greenlee's 0.27 ha (30 m x 90 m) plots as estimated from Greenlee's map and methods description. Like Greenlee's, our layout was based on only two plots, one each in Horse Cove and Poplar Cove, with subplots throughout.

We utilized a modified version of the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998). We chose this protocol with its multiple sample scales because species response to stand age class may vary depending on factors sensitive to scale (Elliot and Loftis 1993, Gilliam 2002).

We subdivided our two 20 m x 50 m CVS plots into ten 10 m x 10 m modules. We put eight sets of nested subplots (including subplots of 0.01 m², 0.1 m², 1 m², 10 m²) in four interior modules. We also included additional non-nested subplots in the corners of some of the remaining modules (Figure 1), resulting in subplot counts of: 13 at 0.01 m², 11 at 0.1 m², 11 at 1 m², 13 at 10 m², and 10 at 100 m². For each species, we calculated frequency of occurrence at the 1 m² scale (number of 1 m² subplots of occurrence ÷ 11 total subplots). We used the Sørensen Indices, shared species presence divided by total species presences (Barbour et al. 1999, McCune and Grace 2002), to calculate community coefficients. Then we calculated Bray-Curtis coefficients (also referred to as weighted Sørensen Indices) by applying herbaceous cover estimates to these calculations (McCune and Grace 2002).

We assessed species richness for subplots at scales 100 m² and below. All vascular plants rooted in a given plot were considered present. Plant taxonomy followed Weakley (2006), augmented by Radford et al. (1968) as needed. Our USFS collection permit prohibited collection of species with five or fewer individuals at a given location, which hampered our identification of some infrequent species left as “unknowns”. The authors deposited voucher specimens at the NCSC herbarium in Raleigh, North Carolina.

We estimated percentage cover for the herbaceous layer in all ten modules (100 m² scale) using the CVS cover classes (Table 2). To facilitate comparison with Greenlee’s data, we departed from standard CVS procedures; our cover estimates reflected only the herb stratum (< 1 m), and not cover contributed by shrub and tree strata. The representative percentage coverage for a module was derived as the midpoint between the high and low area for a given cover value (Table 2). We averaged these midpoint values across all ten 100 m² subplots to get a single 0.1 ha percentage cover value.

We identified trees as those stems with a diameter at breast height (dbh, 1.4 m high) \geq 10 cm. For these stems we calculated basal area and stem density (total stems sampled in the 0.1 ha plot, multiplied by 10 to yield stems/ha).

We used Ulrey's (2002) constancy tables (species lists) to identify rich cove indicator species. Ulrey (2002) described 11 major southern Appalachian regional community types below 4500 ft (1372 m) in elevation, including the rich cove community type (pp. 48 – 52). For the rich cove community type, he listed the 68 species with greatest mean cover in the community. Ulrey (2002) described five subtypes of rich cove, with species listings for each subtype. Using Ulrey's (2002) lists, we defined rich cove indicator species as those species with high specificity to the rich cove community, and also high constancy within the rich cove community subtypes. We created two categories of indicator species, which we called “excellent” and “good”. There were four excellent and 14 good indicator species out of the 68 species in Ulrey's rich cove constancy table. Formulae for calculating these indicator species were:

(1) Excellent indicators occurred in Ulrey's (2002) rich cove + (0 of 10 other regional communities) + (5 of 5 rich cove subtypes).

(2) Good indicators occurred in Ulrey's (2002) rich cove + (\leq 1 of 10 other regional communities) + (\geq 4 of 5 rich cove subtypes).

Different historical records indicated that Horse Cove was cut in either 1939 or 1956 (Greenlee 1974, Duffey and Meier 1992, USFS personal communication). To clarify stand age, we received USFS permission to core 3 dominant trees near our study site in Horse Cove. In June 2005, we cored two *Liriodendron tulipifera* and one *Tilia americana*, which yielded breast height ring counts of 53, 48, and 52 respectively. These cores suggested a timber harvest in 1956 when these trees were saplings. This finding corroborates to

Greenlee's estimate based on discussions with Joyce Kilmer management personnel in 1972 (Greenlee 1974 and personal communication).

We used Statistical Analysis System (SAS) software (version 9.1.2) to identify differences in species richness between sites. We investigated the shape and intercept of the species-area relationship using the General Linear Model (GLM) procedure in SAS. The species-area curves for each plot were constructed using the average richness of all subplots at a given scale (0.01 m², 0.1 m², 1 m², 10 m², and 100 m²) and the point estimate at 1000 m².

Fridley et al. (2005) found that the Arrhenius model (log species: log area) provided the best fit of a species-area curve for small scales up to 1000 m². Therefore, we used the log transformations of species richness and scale (area) to determine slope (rate of species accumulation) and intercept. To gain greater replication for our species-area analysis, we incorporated data from Newell et al.'s (1997) two closest sites in each cove (plots labeled 514, 553, 678, and 679). These sites were located 100 m to 200 m away from our plots, and contained similar vegetation. We calculated a separate slope and intercept for each our two plots, as well as the four Newell et al. plots; this provided three slopes and intercepts from each cove. We averaged the three slopes and intercepts for each cove, and we conducted two-tailed t-tests of slopes and intercepts between coves.

When calculating species-area regression lines for the rich coves, we found that the smallest spatial scale (0.01 m²) acted as a highly influential point. Regressions incorporating the 0.01 m² scale had r² values of approximately 0.95, while regressions without the 0.01 m² scale had r² values of around 0.98. The poorer fit for models including the 0.01 m² scale appeared to be the result of reduced richness at this scale. Rich cove 0.01 m² subplots had a low species capture because the size of the mega-forbs in the herb layer. Large individual

plants resulted in infrequent rooting in the 0.01 m² plots, even though the plots frequently had herbaceous cover. Inclusion of the 0.01 m² scale for the rich cove regressions increased slopes and reduced intercepts. For these reasons, we conducted regression analysis using data from spatial scales of 0.1 m² to 1000 m². This included recalculating Fridley et al.'s (2005) regional slope and intercept.

RESULTS and DISCUSSION

We found no differences in the species-area relationships between Poplar Cove and Horse Cove in either slope or intercept ($p = 0.198$ and $p = 0.487$, respectively). Because there were no differences, we averaged all six slopes and intercepts for a localized rich cove average (log₁₀ species: log₁₀ area regression of $y = 0.372x + 0.934$) (Table 3). When we compared this model to Fridley et al.'s (2005) regional model, there was no difference in the rate of species accumulation ($p = 0.096$ for slope), but the rich coves had significantly higher species richness at all scales ($p = 0.008$ for intercept). These findings corresponded with the widely-accepted view that the rich cove community has higher species diversity than the regional norm (Braun 1950, Ulrey 2002, Simon et al. 2006). This high species diversity is supported by the complex topography, high rainfall, and microsite variation of the coves and may also be high because the southern Appalachians acted as a refuge for many plant species during the advance and retreat of previous ice ages (Whittaker 1956, Pittillo et al. 1998).

Within our two plots, we encountered 137 species (Table 4), with 67 species common to both. At the 0.1 ha scale in Poplar Cove and in Horse Cove, we encountered all four excellent indicators species (*Caulophyllum thalictroides*, *Laportea canadensis*, *Osmorhiza claytonia*, and *Trillium erectum*), although *L. canadensis* and *O. claytonia* had only trace occurrences ($\leq 0.01\%$ mean cover at the 0.1 ha scale) in Poplar Cove. Similarly, 13 of 14

good indicators occurred in each plot, although in each case, three of these good indicator species had only trace occurrences. We also compared our species lists with species lists from acidic cove forest, red oak-montane oak hickory forest, and other related communities (Schafale and Weakley 1990, Newell et al. 1997, Ulrey 2002). Based on the high number of rich cove indicator species and the absence of key species from other communities, we concluded both plots were from the rich cove community.

The Sørensen index (Table 5) for the two plots was 66. Coefficients of 50 or more represent the same association (Barbour et al. 1999). Our additional investigation of the similarity of the herbaceous layers resulted in a Bray-Curtis coefficient of 43. Together, these indices indicated that the Poplar Cove and Horse Cove plots reflected the same rich cove association, but with different expressions of dominance in the herbaceous layer.

The Horse Cove tree layer had half as many species as Poplar Cove (5 versus 10) (Tables 6a and 6b). Diameter distributions in Horse Cove reflected a normal distribution centered on a cohort of *Liriodendron tulipifera* ranging from 30 to 50cm dbh (Figure 2)¹. By contrast, Poplar Cove had an inverse-J shape diameter distribution with trees reaching diameters over 60 cm (we found at least 2 stems over 100 cm dbh within 100 m of our site). The inverse-J diameter distribution with high species diversity in the canopy epitomizes a climax rich cove forest, presumably at basal area carrying capacity (Greenberg et al. 1997, Hardt and Swank 1997). Poplar Cove also had nearly ten percent greater basal area than Horse Cove (40.3 and 36.3 m²/ha, respectively). Assuming a similar site index for both sites, then Horse Cove appeared to be approaching carrying capacity.

¹ We attempted to fit diameter distribution curves using multiple distributions, such as the Weibul; however, our sample size was too small to fit significant curves for these data.

As previously noted, in selecting our study plots, we attempted to center our 0.1 ha plots inside Greenlee's study areas. Based on the differences in total basal area and the species with the greatest stem density, we concluded that our Poplar Cove plot center was likely 10 to 20 meters upslope of Greenlee's plot center (bounded downslope by an ephemeral stream). Inspection of the site showed that the largest *L. tulipifera* and the greatest number of *Halesia tetraptera* were close to the local drainage. Moving upslope, there was a shift to somewhat smaller diameter *Liriodendron* and increasing dominance of *Tsuga canadensis* in the understory. These field observations of shifting overstory and understory dominance correspond to the differences found between the tree data from Greenlee's 1972 survey (Greenlee 1974) and our own survey in 2003 (Table 6a), and suggest little change in the tree layer.

The plot overlap between the 1972 and 2003 samplings of Horse Cove's tree layer appeared better than those of Poplar cove (Table 6b). *Liriodendron tulipifera* dominated the canopy in both cases and contributed about 80% of the basal area and 90% of the canopy. *Halesia tetraptera* dominated the understory. *Halesia tetraptera* and *Acer pensylvanicum* appeared to have capitalized on the recent demise of *Cornus florida*.

We compared the frequency of occurrence of species at the 1 m² scale between the 1972, 1995, and 2003 samples (Greenlee 1974 and Newell et al. 1997; Table 4). Only six species in Horse Cove (*Acer rubrum*, *Halesia tetraptera*, *Laportea canadensis*, *Phegopteris hexagonoptera*, *Tiarella cordifolia*, *Toxicodendron radicans*) and four species in Poplar Cove (*Eurybia divaricata*, *Parthenocissus quinquefolia*, *Quercus rubra*, and *Thelypteris noveboracensis*) maintained a frequency of occurrence of greater than 0.1 across all three samplings. *Toxicodendron radicans* was the most notable species in this comparison, as it

had the highest consistent frequency throughout the Horse Cove samples, but was never detected in the 1 m² samples in Poplar Cove. *T. radicans* does occur in older rich cove communities, but these data appear to demonstrate its opportunistic abilities to establish and perpetuate dominance post-disturbance. None of the other species showed such noticeable difference in 1 m² frequency of occurrence between sites. Most species showed variation in frequency of occurrence, suggesting species turnover between samplings.

Microenvironmental gradients probably had substantial effects on herbaceous distributions (Bratton 1976, Beatty 1984). Changes in microenvironments during the years between studies may have caused variation in herbaceous dominance. Rich coves have high species density across the measured spatial scales. High species density leads to increased competition and may also have contributed to species turnover between 1972, 1995, and 2003.

We compared species density at the 1 m² scale over the 31 year period, using data from Greenlee (1974), Duffey and Meier (1992), Newell et al. (1997), and our survey (Table 7). We calculated the species density in Greenlee's herbaceous plots based on his frequency data ([frequency / relative frequency] X 100). Variation in study designs may have been a factor in the species density differences between the four studies. For example, Greenlee (1974) used rectangular quadrats (.25 m x 4 m), while the other three studies used square quadrats (1 m x 1 m). Rectangular plots incorporate greater microsite variation and elevated Greenlee's total species capture at the 1 m² scale. Additionally, Greenlee (1974), Newell et al. (1997), and we used systematic emplacement methods for our 1 m² quadrats, sampling even in areas of low species presence like on large rocks, or under *Tsuga canadensis* saplings. Duffey and Meier (1992) may have avoided such areas of low diversity, much as

they avoided *Rhododendron* patches. To adjust for sampling differences, we have also shown the Horse Cove species richness as a relative value for each given study (Horse Cove species richness \div by Poplar Cove species richness) (Table 7). These studies suggest that Horse Cove species density declined after age 16 and rebounded after age 35.

To further develop our concept of species richness changes during rich cove succession, we reviewed related articles by Elliott et al. (1997) and Ford et al. (2000). Elliott et al. (1997) found that in a cove-hardwood stand biodiversity peaked at age 2, and then declined through age 16. This decline reflected loss of successional shade-intolerant species (*Erechtites* Rafinesque, *Solidago* L., *Eupatorium* L., *Panicum* L., and *Aster* L.) before late successional, shade-tolerant species (*Viola* L., *Galium* L., *Sanguinaria* L., *Uvularia* L., and *Veratrum* L.) had become well established (Elliott et al. 1997). Elliott et al. (1997) observed that ground flora species diversity and richness in 16 year old cove-hardwoods were both lower than those in neighboring 30 year old cove-hardwoods. Ford et al. (2000) found no statistical difference in species richness at the 1 ha scale between cove-hardwoods aged 15, 25, 50, and ≥ 85 , although their data suggest a trend of increasing species richness in the later age classes.

Variation in species composition and density reflects shifting importance between early succession and late succession species (Horn 1974, Hunter 1990, Elliott et al. 1997). Sometime after canopy closure, favorable environmental conditions return and late-succession species repopulate to higher frequencies (Horn 1974). Following this example, we concluded that by age 39 years the 1 m² species richness in Horse Cove had returned to a level no different from that of the Poplar Cove old growth.

An additional and dramatic change in these sites resulted from disease. Dogwood anthracnose, *Discula destructiva* (Redlin), locally extirpated *Cornus florida* L.. Based on Newell et al. (1997), *C. florida* remained a prominent understory component in both coves through 1995. We found dead stems still standing in 2003, but none still alive in or around our plots. *Acer pensylvanicum*, *Halesia tetraptera*, and to a lesser extent *Cornus alternifolia* apparently filled the niche vacated by *Cornus florida*. Furthermore, Hemlock woolly adelgid, *Adelges tsugae* (Annand) had become established by 2005 (none was noticed during our initial survey in 2003). All the *Tsuga canadensis* that we inspected in 2005 had the adelgid and appeared to be in decline. The loss of *Castanea dentata*, *Cornus florida*, and pending loss of *Tsuga canadensis* may have future community effects not yet apparent.

We found that these two sites had similar vegetative communities. Numerous authors (Braun 1950, Schafale and Weakley 1990, Ulrey 2002) note the wide variation in species within the rich cove community type, and both of our sites fall within these tolerances. By age 47 years, Horse Cove had neither reduced species richness nor atypical community composition compared to the neighboring old growth in Poplar Cove. Differences in herbaceous dominance (percentage cover) most probably arose from successional distinctions between the two sites, natural variation within the rich cove community type, and differences of microenvironment.

Braun (1950) noted that separated stands often appear to differ from each other because of the high number of species which occur in coves and the relatively small size of individual stands. This is reinforced by Ulrey, who reported that 262 species occurred in at least 2.5% of the 188 rich cove plots (0.1 ha each) which he reviewed (Ulrey 2002). Other studies focused primarily on tree species have shown that old growth rich coves are not static

in species composition (Greenberg et al. 1997, Runkle 1998, Busing 1998). Our comparison of data from 1972, 1995, and 2003 suggest that within a rich cove, frequencies of occurrence for individual species at the 1 m² scale were quite dynamic over distances of less than 200 m and through time. Furthermore, the rich cove herbaceous layer appeared more highly variable over time than did the tree layer. These data suggest responses of individual species to stochastic changes consistent with the Gleasonian model, and with faster turnover in the herbaceous layer reflecting the shorter lifecycle of herbs.

Researchers still cannot definitely determine how long it may take to fully transition from an even-aged stand like Horse Cove, to the gap dynamics of old growth like Poplar Cove (Busing 1998, Runkle 1998). Duffey and Meier (1992) and Meier et al. (1995) claim that the process of logging and divergence from gap phase regeneration provides multiple vectors to reduce biological diversity among vernal herbs. We examined the complete suite of species and found that most of the major species overlapped both sites, although the importance of individual species varied. However, patch size and proximity of late-succession species pools probably influenced the rate of recovery for individual species and overall richness (Pearson et al. 1998, Ford et al. 2000).

Comparisons of these two sites ultimately led us to conclude that assessing impacts to rich cove biodiversity must go beyond species-area or community level relationships. Managers need specific information on individual species responses in order to allow them to account for natural or management impacts on biodiversity. In order to assess differences in species frequency of occurrence due to long term logging effects, future studies will require substantial replication across many sites and at multiple scales. Once researchers can

identify individual at-risk species, they may determine mechanisms responsible for risk and help find means for mitigation.

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TABLE 1. Areas of Old Growth Compatible Forests & Mixed Mesophytic Forest of southern Appalachian National Forests.

	Total Area (ha)	Old Growth Compatible Area (ha)	Mixed Mesophytic Area (ha)
Chattahoochee (GA)	257,788	60,632 (24%)	14,249 (6%)
Nantahala & Pisgah (NC)	421,665	129,783 (31%)	37,191 (9%)
Cherokee (TN)	244,305	146,208 (60%)	37,306 (15%)
TOTAL	923,758	336,623 (36%)	88,746 (10%)

* Data derived from USDA Forest Service 1994 (Appendix K), 2004a (Appendix D), and 2004b (Appendix D).

**TABLE 2. Cover Values for
CVS Protocol (Peet et al. 1998)**

Cover Value	Low range (m ²)	High range (m ²)
1	0	0.1
2	0.1	1
3	1	2
4	2	5
5	5	10
6	10	25
7	25	50
8	50	75
9	75	95
10	95	100

**TABLE 3. Species-Area Relationships of Joyce Kilmer rich coves and the regional average:
t-Test Comparison of Regression Slope and Intercepts**

	N	Mean	Standard Deviation	d.f. Satterthwait	P Value	Test Power
Slope	6 Joyce Kilmer rich coves (Poplar and Horse Coves)	0.372	0.042			
	1472 Regional Average (Fridley et al. 2005)	0.337	0.082	5.16	0.096	0.383
Intercept	6 Joyce Kilmer rich coves (Poplar and Horse Coves)	0.934	0.099			
	1472 Regional Average (Fridley et al. 2005)	0.766	0.309	5.4	0.008	0.891

* Slope and intercept calculated SAS 9.1.2 software, using log10 species count and log 10 area.

TABLE 4. Species List with Mean Frequency of Occurrence (at 1 m² scale) and Percentage Cover (at 100 m² scale)

Tree & shrub species	Frequency of Occurrence						Percentage Cover	
	Poplar Cove			Horse Cove			Poplar Cove	Horse Cove
	1972	1995	2003	1972	1995	2003	2003	2003
<i>Acer pensylvanicum</i> L.		0.06	0.09	0.06	0.19		0.65%	0.54%
<i>Acer rubrum</i> L.	0.05	0.06	0.82	0.83	0.13	0.36	0.45%	0.50%
* <i>Acer saccharum</i> Marshall	0.60	0.13			0.13		0.01%	0.28%
* <i>Aesculus flava</i> Solander		0.06					0.06%	0.00%
<i>Amelanchier laevis</i> Wiegand		0.06	0.09				0.02%	0.17%
<i>Betula alleghaniensis</i> Britton				0.11				
<i>Betula lenta</i> L.					0.06	0.09	0.00%	0.12%
<i>Calycanthus floridus</i> L.					0.06			
<i>Carpinus caroliniana</i> Walter							0.06%	0.00%
* <i>Carya cordiformis</i> (Wagenheim) K. Koch						0.09	0.07%	0.13%
<i>Carya glabra</i> (P. Miller) Sweet			0.09	0.11	0.19	0.09	0.39%	0.39%
<i>Carya ovata</i> (Miller) K. Koch		0.13			0.06			
<i>Castanea dentata</i> (Marshall) Borkhausen		0.13	0.09				0.92%	0.11%
* <i>Cornus alternifolia</i> L.							0.11%	0.34%
<i>Cornus florida</i> L.	0.15			0.39			0.00%	0.17%
<i>Fagus grandifolia</i> Ehrh.	0.10		0.18				0.33%	0.06%
<i>Fraxinus americana</i> L.	0.20	0.06	0.18	0.44	0.13		0.25%	0.55%
<i>Halesia tetraptera</i> Ellis	0.20		0.09	0.11	0.06	0.27	0.48%	1.17%
<i>Hammamelis virginiana</i> L.	0.05	0.06			0.13			
<i>Hydrangea arborescens</i> L.		0.06	0.27	0.11		0.27	0.54%	0.45%
<i>Kalmia latifolia</i> L.			0.09				0.06%	0.00%
<i>Lindera benzoin</i> (L.) Blume	0.05			0.06			0.06%	0.22%
<i>Liriodendron tulipifera</i> L.	0.20			0.72	0.06	0.09	0.01%	0.77%
* <i>Magnolia acuminata</i> L.	0.05	0.06					0.06%	0.00%
<i>Magnolia fraseri</i> Walter				0.06			0.44%	0.22%
<i>Nyssa sylvatica</i> Marshall		0.13					0.00%	0.27%
<i>Oxydendrum arboreum</i> (L.) DC.							0.02%	0.00%
<i>Pinus strobus</i> L.					0.06			
<i>Prunus pensylvanica</i> L.							0.06%	0.00%
<i>Prunus serotina</i> Ehrh.	0.05	0.19	0.09			0.09	0.01%	0.34%
<i>Pyralaria pubera</i> Michx.					0.13			
<i>Quercus montana</i> Willd.							0.01%	0.00%
<i>Quercus rubra</i> L.	0.15	0.13	0.36	0.28			0.45%	0.19%
<i>Robinia pseudoacacia</i> L.							0.11%	0.00%
<i>Sassafras albidum</i> (Nutt.) Nees				0.11			0.01%	0.00%
* <i>Tilia americana</i> L. var. <i>heterophylla</i> (Vent.) Loud.	0.65		0.18	0.11			0.93%	0.21%
<i>Tsuga canadensis</i> (L.) Carrière					0.06		0.08%	0.21%
<i>Vaccinium</i> sp. L.							0.06%	0.00%
<i>Viburnum acerifolium</i> L.				0.11			0.38%	0.00%

TABLE 4. Cont.

Herbaceous species	Frequency of Occurrence						Percentage Cover	
	Poplar Cove			Horse Cove			Poplar Cove	Horse Cove
	1972	1995	2003	1972	1995	2003	2003	2003
<i>Actaea podocarpa</i> DC	0.85			0.11			0.52%	0.06%
* <i>Actaea racemosa</i> L.		0.13	0.09		0.13	0.27	0.62%	0.78%
<i>Actea pachypoda</i> Elliott							0.01%	0.00%
<i>Adiantum pedatum</i> L.	0.05			0.06		0.09	0.49%	0.50%
<i>Ageratina altissima</i> (L.) King & H.E. Robins.	0.05			0.33				
<i>Agrimonia parviflora</i> Aiton				0.17				
<i>Amphicarpa bracteata</i> (L.) Fernald	0.20	0.13		0.61	0.19	0.09	0.00%	0.39%
<i>Anemone quinquefolia</i> L.	0.20		0.27	0.50	0.06		0.01%	0.00%
<i>Anemonella thalictroides</i> (L.) Spach	0.85		0.36	0.17	0.38	0.36	0.60%	0.35%
<i>Aralia racemosa</i> L.							0.11%	0.01%
<i>Arisaema triphyllum</i> (L.) Schott	0.05		0.18	0.44	0.19	0.09	0.14%	0.08%
<i>Aristolochia macrophylla</i> Lam		0.25			0.19	0.64	0.00%	0.65%
<i>Asarum canadense</i> L.	0.05	0.25	0.09				0.01%	0.00%
Asteraceae L.							0.01%	0.00%
<i>Astilbe biternata</i> (Vent.) Britton	0.05						0.53%	0.22%
<i>Athyrium asplenoides</i> (Michx.) AA					0.19			
* <i>Botrychium virginianum</i> (L.) Swartz	0.15	0.13		0.33	0.13	0.55	0.07%	0.55%
<i>Cardamine concatenata</i> (Michx.) Ahles	0.10							
<i>Cardamine diphylla</i> (Michx.) Wood		0.06	0.09	0.17	0.06	0.55	0.17%	0.45%
<i>Carex digitalis</i> Willd.					0.06			
<i>Carex pennsylvanica</i> Lamarck							0.07%	0.01%
<i>Carex plantaginea</i> Lamarck	0.10						0.01%	0.00%
<i>Carex sp.</i> 1 L.			0.09				0.01%	0.00%
<i>Carex sp.</i> 2 L.							0.01%	0.01%
** <i>Caulophyllum thalictroides</i> (L.) Michx.	0.20			0.06			0.36%	0.39%
<i>Chionanthus virginicus</i> L.							0.00%	0.12%
<i>Circea canadensis</i> (L.) Hill	0.10					0.09	0.00%	0.11%
<i>Clematis sp.</i> L.				0.06				
<i>Clintonia umbellulata</i> (Michx.) Morong			0.27		0.13		0.60%	0.01%
* <i>Collinsonia canadensis</i> L.	0.05		0.18				0.18%	0.01%
<i>Conopholis americana</i> (L.) Wallroth		0.06					0.06%	0.00%
Cyperaceae				0.11				
<i>Cypripedium acaule</i> Aiton						0.09	0.01%	0.34%
<i>Dennstaedtia punctilobula</i> (Michx.) T. Moore				0.17		0.09	0.00%	0.39%
<i>Deparia acrostichoides</i> (Sw.) M.Kato							0.06%	0.00%
<i>Desmodium nudiflorum</i> (L.) DC.		0.38	0.55		0.25		0.50%	0.11%
<i>Dichanthelium boscii</i> (Poir.) Gould & C.A. Clark							0.00%	0.01%
<i>Dioscorea c.f. villosa</i> (Walter) J. F. Gmel.	0.05	0.19	0.09	0.28	0.13		0.55%	0.07%
<i>Dryopteris intermedia</i> (Muhlenberg ex Willd.) A. Gr.	0.10	0.25						
* <i>Dryopteris marginalis</i> (L.) A. Gray	0.10				0.06		0.23%	0.06%
<i>Erigeron pulchellus</i> Hook							0.01%	0.00%
<i>Euonymus americanus</i> L.			0.09		0.25		0.17%	0.17%
<i>Euonymus obovatus</i> Nutt.		0.38						
<i>Eupatorium purpureum</i> L.						0.09	0.00%	0.19%
<i>Eupatorium sp.</i> 1 L.			0.09				0.18%	0.00%
<i>Eupatorium sp.</i> 2 L.			0.09				0.13%	0.00%
<i>Eurybia divaricata</i> (L.) Nesom	0.50	0.13	0.55		0.06	0.09	0.69%	0.39%
<i>Galearis spectabilis</i> (L.) Raf.				0.17	0.06		0.01%	0.01%
<i>Galium aparine</i> L.	0.30			0.06				
<i>Galium circaeans</i> Michx.						0.18	0.13%	0.25%
<i>Galium latifolium</i> Michx.	0.75	0.06		0.39			0.07%	0.00%

TABLE 4. Cont.

Herbaceous species	Frequency of Occurrence						Percentage Cover	
	Poplar Cove			Horse Cove			Poplar Cove	Horse Cove
	1972	1995	2003	1972	1995	2003	2003	2003
* <i>Galium triflorum</i> Michx.					0.06		0.01%	0.06%
<i>Geranium maculatum</i> L.			0.09	0.06			0.45%	0.00%
<i>c.f. Geum</i> sp L.							0.00%	0.01%
<i>Geum</i> sp. L.					0.27		0.00%	0.50%
<i>Goodyera pubescens</i> (Willd.) R. Brown	0.05	0.06	0.09	0.13			0.08%	0.13%
<i>Hepatica acutiloba</i> Augustin de Candolle	0.80			0.19				
<i>Heuchera villosa</i> Michx.		0.06						
<i>Hydrophyllum canadense</i> L.	0.05	0.13					0.00%	0.01%
* <i>Impatiens capensis</i> Meerburg		0.25						
<i>Impatiens pallida</i> Nutt.				0.06				
<i>Iris cristata</i> Ait.	0.05						0.06%	0.00%
Lamiaceae sp. 1 Lindley			0.09				0.01%	0.00%
Lamiaceae sp. 2 Lindley							0.01%	0.00%
** <i>Laportea canadensis</i> (L.) Weddell	0.50	0.31		0.22	0.13	0.27	0.00%	0.18%
<i>Lilium superbum</i> L.							0.13%	0.00%
<i>Lysimachia quadrifolia</i> L.		0.06		0.06				
<i>Maianthemum racemosum</i> (L.) Link		0.13	0.36		0.19		0.74%	0.06%
<i>Medeola virginiana</i> L.		0.06	0.55	0.17		0.18	1.52%	0.39%
<i>Melanthium parviflorum</i> (Michx.) S. Watson	0.55	0.06	0.45	0.06	0.13		0.65%	0.45%
<i>Mitchella repens</i> L.			0.09		0.13		0.21%	0.00%
** <i>Osmorhiza claytonii</i> (Michx.) C.B.	0.25						0.01%	0.25%
<i>Panax quinquefolium</i> L.							0.19%	0.07%
<i>Parthenocissus quinquefolia</i> (L.) G. Planch.	0.45	0.81	0.18	0.56	0.19	0.09	0.63%	0.40%
<i>Phegopteris hexagonoptera</i> (Michx.) Fee	0.10	0.06	0.55	0.17	0.13	0.18	0.50%	0.34%
<i>Poa compressa</i> L.							0.01%	0.00%
<i>Poa</i> sp. L.	0.20			0.06			0.01%	0.00%
<i>Podophyllum peltatum</i> L.	0.05				0.06	0.09	0.01%	0.24%
<i>Polygonatum biflorum</i> (Walter) Elliott		0.06	0.73		0.19	0.18	0.94%	0.40%
<i>Polystichum acrostichoides</i> (Michx.) Schott	0.15		0.27		0.50	0.73	0.88%	4.71%
<i>Potentilla canadensis</i> L.				0.06	0.25			
<i>Prenanthes</i> sp. L.		0.13	0.27		0.19	0.09	0.89%	0.24%
<i>Prenanthes trifoliata</i> (Cassini) Fernald	0.10			0.28				
<i>Prosartes lanuginosa</i> (Michx.) D. Don	0.20		0.36	0.06	0.25		1.23%	0.29%
<i>Ranunculus hispidus</i> Michx.					0.25		0.06%	0.00%
<i>Ranunculus recurvatus</i> Poir.				0.44				
<i>Ribes cynosbati</i> L.		0.06						
<i>Rubus canadensis</i> L.							0.15%	0.00%
<i>Rubus</i> sp. L.				0.11			0.00%	0.06%
<i>Rudbeckia</i> sp. L.				0.06			0.00%	0.17%
<i>Sanguinaria canadensis</i> L.	0.05				0.19		0.22%	0.50%
<i>Sanicula canadensis</i> L.					0.06		0.00%	0.23%
<i>Sanicula odorata</i> (Rafinesque) KM Pryer & LR Phillip	0.40			0.11			0.00%	0.44%
<i>Sanicula</i> sp. L.			0.09			0.09	0.01%	0.00%
<i>Scutellaria elliptica</i> Muhlenberg ex Sprengel		0.13		0.17				
<i>Scutellaria ovata</i> Hill						0.09	0.02%	0.07%
<i>Silene stellata</i> (L.) Aiton f.		0.06						
<i>Smilax glauca</i> Walt.			0.09	0.11			0.01%	0.08%
<i>Smilax rotundifolia</i> L.	0.20		0.27	0.39	0.13		0.12%	0.55%
<i>Smilax</i> sp. L.							0.36%	0.00%
<i>Solidago caesia / curtisii</i> L.		0.63	0.27		0.18		0.30%	0.24%
<i>Solidago flaccidifolia</i> Small		0.06						

TABLE 4. Cont.

Herbaceous species	Frequency of Occurrence						Percentage Cover	
	Poplar Cove			Horse Cove			Poplar Cove	Horse Cove
	1972	1995	2003	1972	1995	2003	2003	2003
<i>Solidago</i> sp. 2 L.							0.01%	0.00%
<i>Solidago</i> sp.1 L.	0.35			0.44			0.01%	0.00%
<i>Stellaria media</i> (L.) Villars				0.28				
* <i>Stellaria pubera</i> Michx.	0.95				0.25	0.55	0.13%	0.39%
<i>Symphytotrichum retroflexum</i> (Lindl. ex DC.) Nesom					0.06			
<i>Thalictrum clavatum</i> DC.							0.18%	0.00%
<i>Thalictrum dioicum</i> L.		0.13						
<i>Thelypteris noveboracensis</i> (L.) Nieuwland	0.65	0.31	0.73	0.22	0.19	0.09	4.11%	0.48%
* <i>Tiarella cordifolia</i> L.	0.95	0.25		0.44	0.19	0.36	0.00%	0.50%
<i>Toxicodendron radicans</i> (L.) Kuntze				0.72	0.44	0.64	0.00%	0.45%
<i>Trillium cuneatum</i> Raf.			0.09			0.18	0.30%	0.55%
** <i>Trillium erectum</i> L.	0.25		0.45	0.22		0.36	0.45%	0.35%
<i>Trillium grandiflorum</i> (Michx.) Salisb.		0.06			0.19		0.12%	0.00%
<i>Trillium undulatum</i> Willd.		0.13						
<i>Trillium vaseyi</i> Harbison							0.11%	0.18%
Unknown 1							0.01%	0.00%
Unknown 2							0.06%	0.00%
<i>Uvularia perfoliata</i> L.		0.19	0.18	0.22	0.06		0.44%	0.34%
<i>Uvularia sessilifolia</i> L.			0.09				0.28%	0.00%
<i>Viola blanda</i> Willd.		0.13	0.64		0.06		0.65%	0.00%
<i>Viola canadensis</i> L.	0.90	0.06				0.18	0.00%	0.50%
<i>Viola hastata</i> Michx.		0.38	0.64	0.39	0.06	0.27	0.50%	0.23%
<i>Viola pubescens</i> Ait.							0.00%	0.06%
<i>Viola rotundifolia</i> Michx.					0.19			
<i>Viola sororia</i> Willd.				0.89		0.45	0.00%	0.34%
<i>Viola</i> sp. 1 L.							0.01%	0.00%
<i>Viola</i> sp. 2 L.			0.09				0.01%	0.00%
<i>Vitis aestivalis</i> Michx.				0.11				
<i>Vitis cinerea</i> Engelman ex Millardet		0.06						
<i>Vitis</i> sp. L.							0.01%	0.00%

** *Excellent Rich Cove Indicator Species (See text for definition)*

* *Good Rich Cove Indicator Species (See text for definition)*

1972 data from Greenlee (1974)

1995 data from Newell et al. (1997), provided by R.K. Peet & the Carolina Vegetation Survey

TABLE 5. Poplar Cove - Horse Cove Similarity Measures:

Sorensen Index, Community
 (based on presence only) Coefficient

$$\frac{2 * C}{A+B} * 100 = \frac{2 * 67}{114 + 90} * 100 = \mathbf{66}$$

A = Total Number of species in Poplar Cove
 B = Total number of species in Horse Cove
 C = Total number of species in both Poplar and Horse Cove

Bray-Curtis coefficient, Community
 (2 x shared cover ÷ cover of Poplar Cove + cover of Horse Cove) Coefficient

$$\left(\frac{2 * \sum_{j=1}^p \min(a_{ij}, a_{hj})}{\sum_{j=1}^p a_{ij} + \sum_{j=1}^p a_{hj}} \right) * 100 = \frac{2 * 13.13\%}{31.89\% + 29.30\%} * 100 = \mathbf{43}$$

a_{ij} = herbaceous cover of species i in Poplar Cove
 a_{hj} = herbaceous cover of species h in Horse Cove

TABLE 6a. Tree Layer Basal Area and Stem Counts: Poplar Cove

	2003		1972 (Greenlee)	
	Basal Area m/ha	Stems Count stems/ha	Basal Area m/ha	Stems Count stems/ha
<i>Liriodendron tulipifera</i>	12.5	60.0	15.4	30.4
<i>Carya tomentosa</i>	7.8	20.0	1.1	21.7
<i>Tsuga canadensis</i>	5.2	120.0	5.3	43.5
<i>Quercus rubra</i>	5.0	10.0		
<i>Tilia americana</i>	3.7	10.0	11.3	43.5
<i>Acer rubrum</i>	3.4	60.0	0.4	13.0
<i>Oxydendron arborium</i>	1.0	30.0		
<i>Halesia tetraptera</i>	1.0	30.0	4.6	178.0
<i>Acer saccharum</i>	0.5	20.0	3.8	82.6
<i>Magnolia fraseri</i>	0.2	10.0		
<i>Betula lenta</i>			4.2	91.3
<i>Carya cordiformis</i>			2.1	13.0
<i>Fagus grandifolia</i>			1.4	26.1
<i>Aesculus</i>			1.2	13.0
<i>Cornus florida</i>			0.8	56.5
<i>Betula lutea</i>			0.0	4.4
TOTAL	40.3	370.0	51.7	617.0

TABLE 6b. Tree Layer Basal Area and Stem Counts: Horse Cove

	2003		1972 (Greenlee)	
	Basal Area m/ha	Stems Count stems/ha	Basal Area m/ha	Stems Count stems/ha
<i>Liriodendron tulipifera</i>	29.3	210.0	30.7	410.0
<i>Tilia americana</i>	4.6	20.0	0.0	5.0
<i>Betula lenta</i>	1.1	10.0	0.3	10.0
<i>Halesia tetraptera</i>	1.1	70.0	1.1	75.0
<i>Acer pennsylvanica</i>	0.2	10.0		
<i>Quercus rubra</i>			4.3	15.0
<i>Carya cordiformis</i>			1.1	30.0
<i>Acer rubrum</i>			0.8	50.0
<i>Cornus florida</i>			0.6	50.0
<i>Robinia pseudoacacia</i>			0.3	5.0
<i>Prunus serotina</i>			0.2	5.0
<i>Tsuga canadensis</i>			0.1	10.0
<i>Carya glabra</i>			0.1	5.0
TOTAL	36.3	320.0	39.5	670.0

TABLE 7. Average 1m² Scale Species Richness from Four surveys

Study	Stand Age	Poplar Cove 1 m ² Richness	Horse Cove 1 m ² Richness	Horse Cove richness relative to Poplar Cove
Greenlee (1974) *	16 (1972)	15.55	15.22	0.98
Duffey & Meier (1992)	35 (1991)	14.53 (s.e. ± 0.67)	6.04 (s.e. ± 0.59)	0.42
Newell et al. (1997)	39 (1995)	8.50 (s.e. ± 2.13)	8.94 (s.e. ± 2.23)	1.05
Current Study	47 (2003)	13.09 (s.e. ± 1.78)	10.36 (s.e. ± 0.51)	0.79

* Greenlee used rectangular (.25m x 4m) plots that likely resulted in slightly higher 1 m² species richness relative to the square (1m x 1m) plots used in the other three studies.

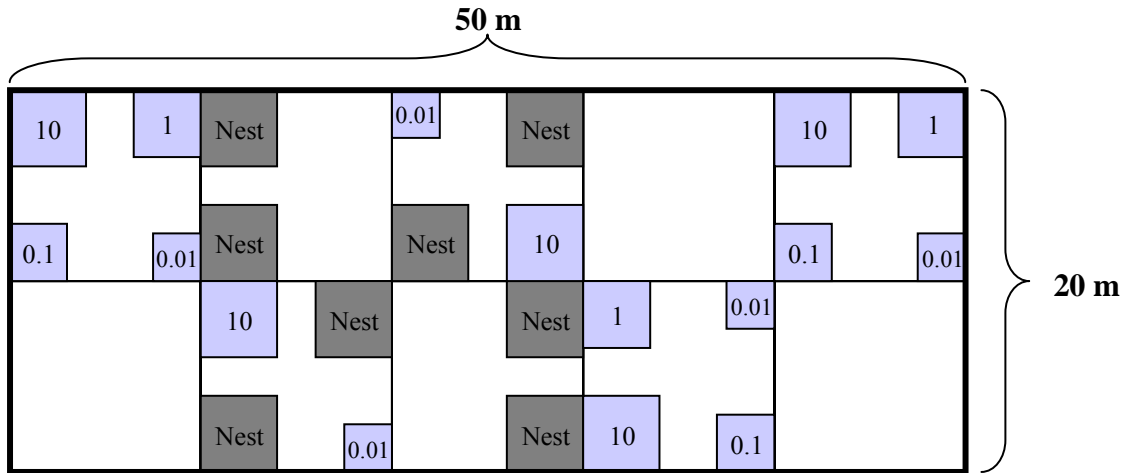


Figure 1. Sampling Design (adapted from the CVS protocol).
 Nested subplots follow Peet et al. (1998) with subplots of 0.01 m², 0.1 m², 1 m², and 10 m²,
 additional plots shown by placement and scale (m²)

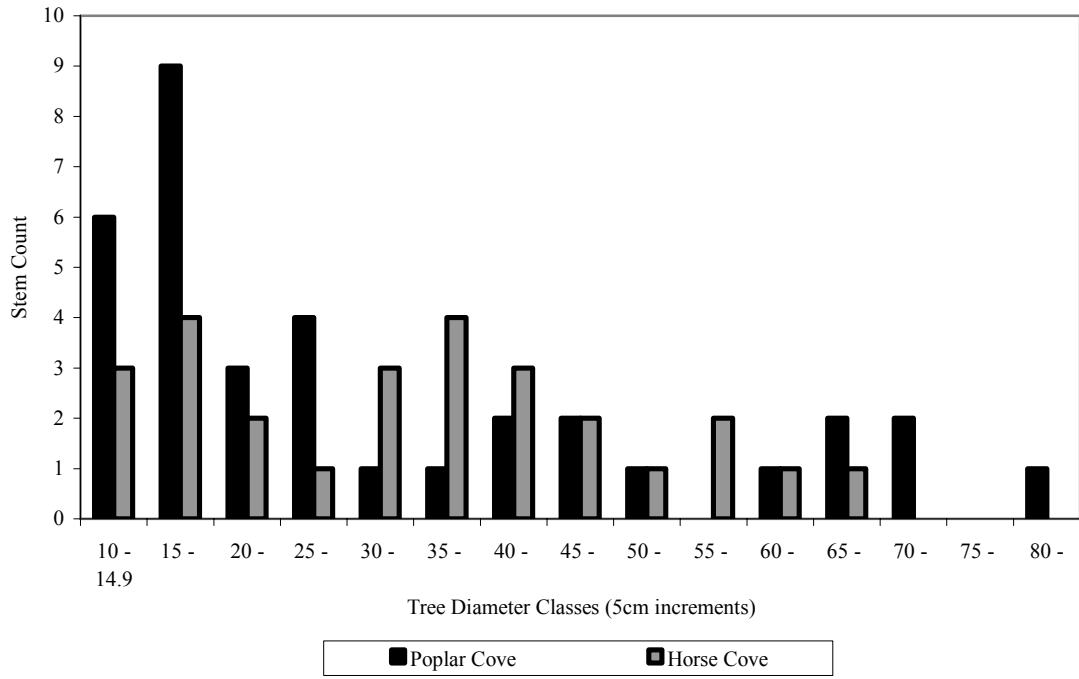


Figure 2. Histogram of Tree Diameters