PATTERNS OF SHIFTING TREE SPECIES COMPOSITION AND DIVERSITY LOSS IN 19 OLD-GROWTH FOREST STANDS IN PENNSYLVANIA

by

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A century of fire suppression and overbrowsing by deer have likely altered patterns of forest regeneration, with detrimental consequences for the future diversity, composition, and function of old-growth stands. We quantified the diversity and composition of tree species in the canopy and understory layers of 19 old-growth stands in Pennsylvania to evaluate the consequences of existing regeneration patterns for the future composition of these communities.

Despite relatively high canopy diversity across all stands, the understory composition of all stands converged to a homogeneous subset of the canopy species. In addition, understory layers had unusually low stem densities, lower species diversity than their respective canopies, and showed a significant lack of mid-tolerant species. Oak species, which often require fire to regenerate, were common in the canopy of 12 stands, but absent from the understory layer of all stands. Our findings suggest that deer browsing and fire suppression are partly responsible for this dramatic alteration of understory species composition. The lower diversity and homogenized species composition of the understory indicates that the future composition of these stands will not resemble the current composition. Alteration of tree species composition is likely to have detrimental effects on the survival of species dependent upon old-growth habitat.

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PREFACE

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1.0 CHAPTER 1

1.1 INTRODUCTION

Old-growth forest stands function as integral components of the contemporary forest matrix. Remnant old-growth stands can serve as seed sources for surrounding secondary forests (Keeton and Franklin 2005) and provide habitat for fauna (Welsh 1990) and flora (Whitney and Foster 1988). However, old-growth stands are extremely rare in the eastern United States, comprising < 1% of forested land east of the Mississippi river (Davis 1996). The natural senescence of canopy trees, pathogen-induced mortality (e.g. beech-bark disease, *Cectria coccinea* var. *faginata*, Gavin and Peart 1993), pest outbreak (e.g. hemlock woolly adelgid, *Adelges tsugae*, Orwig et al. 2002), and other mortality-inducing stresses may hasten canopy turnover throughout eastern temperate forests in the coming century.

The conservation and management of remnant old-growth stands requires an understanding of the patterns of regeneration in these stands across all size classes. However, the processes that contribute to patterns of regeneration of old-growth forests are poorly understood because these stands are rare (Davis 1996), have uncertain disturbance histories (McLachlan et al. 2000), and have ecological interactions (e.g. competition) that play out over decades (Pacala et al. 1996). Numerous factors are likely altering the current species composition of eastern old-growth forest stands particularly overbrowsing by white-tailed deer

(*Odocoilus virginianus*, Horsley et al. 2003), suppression of understory fire (Abrams 1992), and the small size and fragmented distribution of remnant old-growth stands (Harper et al. 2005).

Many of the defining features of old-growth stands (e.g. dominance by shade tolerant species, large diameter trees) are the result of long time periods between large-scale disturbances (Keddy and Drummond 1996). Estimated return times for large, stand replacement disturbances range from 500-1500 years from the Great Lakes region through Pennsylvania and northern New York (Canham and Loucks 1984; Seymour et al. 2002). These stands are therefore largely governed by gap-phase disturbance regimes where the understory saplings represent the available species pool to replace dying canopy trees (Oliver and Larson 1996). Under gap-phase disturbance regimes, rapid recruitment into the canopy by recently dispersed seeds is uncommon in temperate forests (Lertzman 1992; Runkle 1998; Webster and Lorimer 2005), and individuals generally show numerous episodes of release and suppression before reaching the canopy (Nowacki and Abrams 1997). Therefore, the absence or low abundance of a species in the understory reduces the likelihood of that species successfully regenerating in the absence of large-scale disturbances (Leak 1970; Runkle 1981; Waggoner and Stephens 1970). A high relative abundance of a species in the understory does not guarantee an increased abundance in the future canopy (White et al. 1985), however, the importance of understory abundances on the likelihood of capturing gap space has been well documented (Fox 1977; Leak 1970; Runkle 1981; Uhl et al. 1988; Waggoner and Stephens 1970). For example, Runkle (1981; 1998) found that the species composition of the understory layer was a good predictor of canopy composition, and Lertzman (1992) found that the likelihood of capturing a gap was proportional to a species representation in the understory layer. Therefore, the existing species composition and size structure of old-growth stands can provide insight about regeneration patterns and the future composition of the canopy.

Existing regeneration patterns across size classes in stands can help identify causal factors impacting regeneration in old-growth forests and serve as a useful tool to inform the management and conservation of these remnant stands. For example, in stands showing patterns of self-replacement two predictions can be made: 1) all, or most, species present in the canopy should be present in the understory and canopy diversity should be similar to understory diversity, or 2) understory diversity may be higher than canopy diversity if numerous understory specialist species are present, or if the understory contains canopy species which do not successfully recruit into the canopy. If stands do not show patterns of self-replacement, they may show patterns of successional replacement, such as a higher relative abundance of shade tolerant species in the understory than in the canopy (Woods 2000b). Pervasive white-tailed deer (*Odocoilus virginianus*) browsing can significantly lower understory stem densities and increase the representation of more browse-tolerant species (e.g. *Acer pensylvanicum, Fagus grandifolia*) in the understory (Banta et al. 2005; Horsley et al. 2003). Lastly, understory fire suppression can cause regeneration failure of fire-tolerant species (e.g. *Quercus* spp) and therefore an absence of these species in the understory, even in stands with high abundance of fire-tolerant species in the canopy (Abrams and Nowacki 1992).

In this study, we compare overstory and understory species compositions of 19 old-growth stands to test the hypothesis that old-growth stands show patterns consistent with canopy species self-replacement (Lorimer 1980; Runkle 1981; Runkle 1998). Predictions of future species composition based on comparisons of canopy and understory layers can produce misleading results due to assumptions of a constant environment, constant disturbance regime, and equivalent rates of growth and mortality amongst species (White et al. 1985). However, by using overstory/understory comparisons across a large number of stands dispersed over a wide area (Fig. 1), we can identify re-occurring regeneration patterns and the factors that may underlie these patterns while accounting for these assumptions. It is difficult to identify common regeneration patterns from the literature, given different study foci and associated sampling methodologies used. Comparisons of stands in the literature are also difficult because most studies sampled one stand; we only found 6 studies that compared more than 5 stands (Leopold et al. 1988; McGee et al. 1999; Runkle 1981; Tyrrell and Crow 1994; Woods and Cogbill 1994; Ziegler 2000). The large number of stands examined in this study allows us to make direct comparisons of regeneration patterns between stands.

1.2 MATERIALS AND METHODS

1.2.1 Study Area

During 2006, we conducted stand-wide surveys of 19 old-growth forest stands throughout Pennsylvania (Fig 1, Table 1). The old-growth stands surveyed are located in three physiographic regions of Pennsylvania: ridge and valley, deep valley Allegheny plateau, and high Allegheny plateau (Fig 1, Table 1, Braun 1950; DCNR 2000). Nine of the stands are hemlock - white pine - northern hardwood forest types and the remaining ten stands are hemlock - red oak - mixed hardwood forest types (Table 1, Braun 1950; Fike 1999). Seven of the stands have had detailed site descriptions (BMNA: Abrams et al. 2001; FCCF: Abrams and Orwig 1996; TANF & HCANF: Hough and Forbes 1943; ASNA: Nowacki and Abrams 1994; SACF:

Orwig and Abrams 1999; SMNA: Zawadskas and Abrahamson 2003), however, the remaining 12 stands have not been previously described. All old-growth stands sampled reside within a matrix of secondary forests and many have experienced limited human-mediated disturbance including understory fires (Abrams et al. 2001; Abrams et al. 1995; Nowacki and Abrams 1994; Orwig and Abrams 1999) and selective logging (pers. obs., Abrams et al. 2001; Lutz 1930; Nowacki and Abrams 1994; Orwig and Abrams 1999).

1.2.2 Sampling design

Stands ranged in size from 2.75 to 1267 hectares, and 0.15 - 19.8% of each old-growth stand area was surveyed for using a system of stratified transects (Table 1). The first transect in each stand was started at a random point at least 50m from the edges of the stand and 17m radius circular plots (0.09 hectares) were located every 200 meters along the transect. Transects were spaced approximately 100 meters apart and no plots were located within 50 meters of the stand edge or a trail. Each 0.09 hectare plot was sampled for living trees ≥ 5cm diameter at breast height (d.b.h., taken at 1.37m), fallen logs ≥ 10cm diameter at one end, and standing snags ≥ 5cm d.b.h. For living trees we recorded species identity and d.b.h., for fallen logs we recorded the diameter at three points (both ends and the middle), and for standing snags we measured the d.b.h. and height, using a laser range-finder (Bushnell® Yardage Pro™ 800 Compact Rangefinder) to estimate the height of snags > 3m tall. Within each 0.09 hectare plot, we sampled a central $100m^2$ circular plot for all living woody stems > 1.4m tall and < 5cm d.b.h.

Snag volume was estimated as a cylinder using the basal area and height, while log volume was estimated with Newton's formula [1], accounting for hollowed portions of logs (Harmon and Sexton 1996).

[1] $$V = L(A_b + 4A_m + A_t)/6$$

where V is the volume, L is the log length, Ab, Am, and At are the areas of the base, middle, and top of the log, respectively.

1.2.3 Statistical Analysis

Stand size structure was divided into three classes for all analyses, canopy (> 25cm d.b.h.), subcanopy (10.1 - 25cm d.b.h.), and understory (≥ 1.4m height - 10cm d.b.h). Because we are interested in comparisons between size layers, we report results based on the analysis of canopy species only (i.e. species with the potential to reach the canopy), excluding understory specialist species such as *Acer pensylvanicum*, *Carpinus caroliniana*, *Cornus florida*, and *Ostrya virginiana*.

1.2.3.1 Diversity

To quantify diversity, we calculated the Shannon diversity index on a per plot basis, as this index weights species equally by their frequency. The Shannon index is

[2] $$\exp H = \exp(-\sum_{i=1}^{S} p_i \ln \ p_i)$$

where S is the total number of species in the plot and p_i is the relative abundance of the i^{th} species (Jost 2006). This is a slightly modified form of the more commonly used Shannon entropy, however it allows for a more direct comparison of diversity between forest stands in this study (Jost 2006).

We used ANOVA to test for differences in diversity among size classes across all stands and within individual stands (Crawley 2002). We used Tukey's honestly significant difference

(HSD) for contrasts of Shannon diversity indices between size classes within each stand (Crawley 2002). We repeated these analyses with the inverse Simpson's diversity index and found the same qualitative results in 18 of 19 contrasts between the understory and canopy size classes and in 47 of the total 57 contrasts (Appendix A). Given the consistency of the results for inverse Simpson's and Shannon index, we only present results for the Shannon's diversity index. Additionally, we used ANOVA to test for differences in species richness among size classes across all stands and within individual stands. We used Tukey's HSD for contrasts of species richness between size classes within each stand.

1.2.3.2 Species composition

Patterns of species composition within and between size classes were assessed with non-metric multidimensional scaling (NMDS) ordination using species abundance data for each size class in each stand (Kenkel and Orloci 1986). Semi-metric Bray-Curtis dissimilarity indices were used for NMDS ordination because it has one of the strongest relationships between site dissimilarity and ecological distance, making it a good measure of ecological distance for species abundance data (Faith et al. 1987). The Bray-Curtis dissimilarity index (BC) is

$$[3] \qquad BC = \frac{\sum_i | X_{ij} - X_{ik} |}{\sum_i (X_{ij} + X_{ik})}$$

where X_{ij} is the abundance of the i^{th} species at site j and X_{ik} is the abundance of the i^{th} species at site k (Krebs 1989).

Nonparametric MANOVA (also called distance-based redundancy analysis) was used to test for differences in species composition between size classes within each stand. Nonparametric MANOVA was used because the high occurrence of zeros in the abundance dataset and the low abundance of rare species violate the assumption of multivariate normality made by parametric MANOVA (Legendre and Anderson 1999; McArdle and Anderson 2001). Furthermore, linear models cannot be fit with parametric MANOVA using semi-metric dissimilarity indices (e.g. Bray-Curtis), as these semi-metric dissimilarity indices violate the triangle inequality property (Legendre and Anderson 1999; McArdle and Anderson 2001). Additionally, the nonparametric MANOVA allowed us to statistically test for differences in species composition using the same dissimilarity index (Bray-Curtis) used in the NMDS ordination. We used three dissimilarity indices (Bray-Curtis, Morista- Horn, Chao) to test for differences in species composition between size classes and to account for possible limitations in the choice of any one dissimilarity index. While the Bray-Curtis dissimilarity index is commonly used as a measure of ecological distance for species abundance data, it is biased by abundant species and can be affected by small sample size (Krebs 1989). To account for each of these potential shortfalls, we used the Chao index, which gives greater weight to rare species than the Bray-Curtis index (Chao et al. 2005), and the Morista-Horn index, which is nearly independent of sample size (Krebs 1989). While we used three dissimilarity indices for our analyses, we only report results for the Bray-Curtis analyses as the other dissimilarity indices gave us qualitatively very similar results.

Lastly, we used nonparametric Kruskal-Wallis tests for comparisons of species relative abundance between canopy and understory layers. All analyses were conducted in R (R_Development_Core_Team 2007), using the muStat package for Kruskal-Wallis tests (Wittkowski and Song 2007), and the vegan package for nonparametric MANOVA, NMDS ordination, and the calculation of Bray-Curtis, Chao, and Morista-Horn indices (Oksanen et al. 2007).

1.3 RESULTS

1.3.1 Diversity and Species Richness

Shannon diversity differed significantly between stands ($F_{18, 693} = 15.0$, $P < 0.001$) and between size classes across all stands ($F_{2,693} = 221.3$, $P < 0.001$). In 17 of 19 stands, diversity differed significantly between size classes (Table 2) and was significantly higher in the canopy than in the understory (Table 2). The ARNA and CSNA stands showed no significant difference in Shannon diversity (ARNA: $F_{2,15} = 0.4$, $P = 0.67$; CSNA: $F_{2,21} = 1.2$, $P = 0.31$) across size classes (Table 2). The subcanopy layer showed an intermediate level of diversity; subcanopy diversity was significantly lower than canopy diversity in 11 of 19 stands, whereas the subcanopy layer was significantly more diverse than the understory layer in only 9 of 19 stands (Fig. 2, Table 2).

Similarly, species richness differed significantly between stands ($F_{18, 693} = 15.1$, $P < 0.001$) and between size classes across all stands ($F_{2, 693} = 226.7$, $P < 0.001$). In 18 of 19 stands, species richness differed significantly between size classes (Table 3) and was significantly higher in the canopy that in the understory (Fig. 3, Table 3). The ARNA stand showed no significant difference in species richness ($F_{2, 15} = 0.42$, $P = 0.66$). The subcanopy layer showed an intermediate level of species richness; subcanopy species richness was significantly lower than canopy species richness in 10 of 19 stands, whereas the subcanopy species richness was significantly higher than the understory layer species richness in 12 of 19 stands (Fig 3, Table 3).

1.3.2 Species Composition

NMDS ordination shows a clear divergence of understory and canopy species composition across all stands, with no overlap of their respective polygons (Fig. 4). Subcanopy species composition overlaps with both the understory and canopy species composition (Fig. 4). The canopy cluster spans a species gradient ranging from sites heavily influenced by oaks (QUAL, *Quercus alba*; QURU, *Q. rubra*; QUVE, *Q. velutina*) to sites strongly influenced by hemlock (TSCA, *Tsuga canadensis*), yellow birch (BEAL, *Betula alleghaniensis*), and black birch (BELE, *B. lenta*). The understory cluster does not show a species gradient as clear as that seen in the canopy cluster, but it does appear that hemlock, beech (FAGR, *Fagus grandifolia*), sugar maple (ACSA, *Acer saccharum*), and red maple (ACRU, *A. rubrum*) strongly influence site positions (Fig. 4).

Species composition significantly differed between size class (F = 13.2, P < 0.001, 1000 permutations) and stands (F = 4.9, P < 0.001, 1000 permutations). In 18 of 19 stands, species composition was significantly different in the understory versus canopy layers (Fig. 5, Table 4). The species composition of the canopy and understory layers did not differ in STCF (F = 1.3, P = 0.20, 1000 permutations), likely due to the dominance of hemlock and birch species across all size classes (Fig. 5).

Differences in species composition between canopy and understory layers are primarily due to four major shifts in species abundance. Oak abundance is significantly lower in the understory than canopy in all 12 stands where oak comprises greater than 10% of the canopy (ARNA, ASNA, BCNA, BMNA, BRNA, CSNA, CTCF, DRNA, JRNA, LJRNA, SACF, WRNA; Fig. 5, Table 5). Additionally, the lower understory abundance of subdominant hardwood species (e.g. *Liriodendron tulipifera*, *Fraxinus americana*, *Carya* spp.) in 5 stands

(ASNA, BRNA, DMCF, FCCF, TANF) contributed to the difference in species composition (Fig. 5, Table 5). Three stands (ARNA, HCANF, and TANF) have significantly higher beech abundance in the understory than in the canopy (Fig. 5, Table 5), due to the extensive proliferation of root sucker sprouts (pers obs). Lastly, hemlock abundance was significantly higher in the understory than canopy of 9 stands (BRNA, CTCF, DMCF, FCCF, FDNA, LJRNA, SACF, SMNA, WRNA; Fig. 5, Table 5). The increased abundance of hemlock in the understory of these stands contributed to higher understory relative abundance of shade tolerant species in 18 stands (Table 6). Shade tolerant species are those species classified by Burns and Honkala (1990) as very tolerant or tolerant of shade. STCF was the only stand which did not show a significant difference in the relative abundance of shade tolerant species between the canopy and understory ($\chi^2_{1df} = 0.3$, $P = 0.59$).

1.4 DISCUSSION

1.4.1 Do these old-growth stands show patterns indicative of canopy self-replacement?

Low disturbance, old-growth forests have long been thought to maintain a stable species composition and structure across size classes, due to the prominence of shade tolerant species in all size classes and the importance of the understory layer in replacing canopy trees (Hough and Forbes 1943; Oliver and Larson 1996; Poulson and Platt 1996). In the absence of less frequent, intermediate- (removal of 10 - 50% of the canopy, Woods 2004) or large-scale (stand-replacing) disturbances, the species composition of the understory is expected to resemble that of the canopy, consisting largely of shade tolerant species capable of long-term persistence while suppressed in the understory. With the exception of one stand, STCF, the stands sampled in this study do not show regeneration patterns expected for canopy self-replacement in low disturbance, old-growth forests. Excluding woody shrubs and understory specialist species (e.g. *Acer pensylvanicum*), understory diversity and species richness were consistently lower than canopy diversity and species richness (Fig. 2, Fig. 3, Table 2, Table 3), contradicting our expectations if these stands were in fact late successional, mature old-growth stands (see below). Only 2 of the 19 stands (ARNA and CSNA) showed no significant difference in Shannon diversity between canopy and understory size classes (ARNA: $F_{2,15} = 0.4$, $P = 0.67$; CSNA: $F_{2,21} = 1.2$, $P = 0.31$) and only 1 stand showed no significant difference in species richness between canopy and understory classes (ARNA: $F_{2,15} = 0.42$, $P = 0.66$).

The lower understory diversity and species richness is due to the absence or significantly lower abundance of oaks and mixed hardwood species in the understory of most stands (Fig. 5, Table 5). The understory species composition differed significantly from the canopy in 18 of 19 stands (Fig. 4, Fig. 5, Table 4). The only stand showing no significant difference in understory and canopy species composition, STCF, was dominated by hemlock and birch in all size classes (Fig. 5, Table 4). The understory of all stands showed a distinct species composition that was different from the canopy in an ordination of species abundances (Fig. 4). In the most detailed studies on the role of species abundance in the understory and patterns of canopy recruitment, Runkle (1981) and Lertzman (1992) found a high degree of similarity in the species composition of the canopy and understory in old-growth stands demonstrating canopy self-replacement under gap-phase disturbance regimes (also, see Kneeshaw and Bergeron 1998). Therefore, significant differences in the canopy and understory species composition in 18 of the 19 stands sampled indicates that in the absence of intermediate or large-scale disturbances, the future species composition of the canopy will differ from the current composition in almost all stands.

Differences in species composition of the understory and canopy were primarily due to 1) the almost complete absence of oak species in the understory in 12 stands with a high abundance of oak in the canopy (Fig. 5, Fig. 6), 2) a significantly lower abundance of subdominant, mixed hardwood species in the understory of 4 stands, 3) a significantly higher understory abundance of beech in 3 stands, and 4) a significantly higher understory abundance of hemlock in 9 stands (Fig. 5, Table 5, see Results for specific references to individual stands). Below, we discuss the likely causes and implications of each of these shifts in species composition.

1.4.2 Factors influencing existing regeneration patterns

In 12 of the 19 stands sampled, we found a high abundance of oaks (10-50% of canopy stems) in the canopy and a complete or near absence of oaks in the understory (Fig. 6), consistent with a growing body of literature documenting failed oak regeneration throughout temperate secondary forests across eastern North America (reviewed in Abrams 1992; Abrams 2003). Evidence from dendrochronology (e.g. Nowacki and Abrams 1997), experimental (e.g. Brose and Van Lear 1998), observational (e.g. Brown 1960), and pollen count (Delcourt and Delcourt 1987) studies suggest that recurring understory fire maintained historically high oak abundance throughout much of the eastern temperate forest. Recurring understory fire is hypothesized to promote oak regeneration by reducing understory competition from both shade tolerant and faster growing species that are less tolerant of fire (Brown 1960; Christensen 1977; Lorimer et al. 1994). Decades of oak regeneration failure have been attributed to twentieth century policies of fire suppression (Abrams 1992), which for example, have led a >50% decrease in the number of fires and area burned in Pennsylvania from 1908 to 1990 (Abrams and Nowacki 1992; Haines et al. 1978). The suppression of periodic understory fire allows fire-sensitive species (e.g. sugar maple, red maple) to regenerate and replace oaks in the understory (Christensen 1977; Lorimer et al. 1994). Therefore, it is likely that the loss of oak and replacement by more shade tolerant species (see below) in the understory of the 12 oak stands is partly due to fire suppression.

Decades of overbrowsing by high white-tailed deer populations is another likely cause of failed oak regeneration, low understory hardwood abundance, and low tree diversity in the understory. Deer densities sufficient to negatively impact tree regeneration have been reported in Pennsylvania since the 1930s (Bjorkbom and Larson 1977; Hough and Forbes 1943; Lutz 1930) and continue to inhibit forest regeneration today (DCNR 2004; Horsley et al. 2003). Deer can reduce understory densities, understory diversity, and increase the relative abundance of browse- and shade-tolerant species (Frelich and Lorimer 1985; Horsley et al. 2003; Waller and Alverson 1997). The understory in our study sites had significantly lower diversity (Fig. 2, Table 2), a high abundance of browse-tolerant species (e.g. *Fagus grandifolia* (Fig. 5), *Acer pensylvanicum*-data not shown), and had low densities of small saplings. Densities of small saplings (1.4m tall to 5cm d.b.h.) averaged 492.3 ± 282.95 (± 1 SE) stems ha^{-1} in the 19 stands sampled, including two stands with considerably higher small sapling densities than the other 17 stands (TANF = 5395 stems ha^{-1}, ARNA = 1500 stems ha^{-1}). Excluding the TANF and ARNA stands, the other 17 stands averaged 144.6 ± 31.62 small saplings ha^{-1}, ranging from 0 - 477.8 small saplings ha^{-1}. Both small sapling density estimates are lower than densities reported for temperate old-growth stands; 622 - 2180 small saplings ha^{-1} for hemlock-northern hardwood stands (Chokkalingam and White 2001; Leopold et al. 1988; Orwig et al. 2001) and 428 - 2010 small saplings ha^{-1} for mesophytic stands (Brothers 1993; Chester et al. 1995; Runkle 1998), indicating that the low small sapling density cannot be attributed solely to long periods of understory suppression. Taken together, the low density of small saplings, low understory diversity, and high understory abundance of browse-tolerant species suggest a long-term negative effect of deer on old-growth regeneration. Furthermore, the negative impacts of deer overbrowsing on regeneration has been documented for 5 of the stands sampled in this study, TANF (Bjorkbom and Larson 1977), HCANF (Lutz 1930), SACF (Orwig and Abrams 1999), BMNA (Abrams et al. 2001), and FCCF (Abrams and Orwig 1996).

Although there is evidence that old-growth forests can maintain diversity and species composition under low severity gap-phase disturbance regimes (Fox 1977; Kneeshaw and Bergeron 1998; Lertzman 1992; Lorimer 1980; Poulson and Platt 1996; Runkle 1981), models of secondary succession predict directional changes in species composition towards increasing abundances of shade tolerant species (e.g. hemlock, beech, sugar maple) and concomitant decrease in both mid-tolerant (e.g. oaks) and shade intolerant species (e.g tulip poplar, white ash) abundance (Connell and Slatyer 1977; Oliver and Larson 1996; Pacala et al. 1996). The higher understory abundance of shade tolerant species in 18 of 19 stands (Table 6) supports evidence from Woods (2000a; 2000b) that old-growth stands continue to show directional replacement of species, even centuries after the last major disturbance event. The high understory abundance of shade tolerant species is largely a result of the higher abundance of hemlock and beech in the understory than canopy (in 9 and 3 stands, respectively; Fig. 5, Table 5). The one stand which did not show a higher understory abundance of shade tolerant species, STCF, was dominated by the shade tolerant hemlock across all size classes (Fig. 5, Table 5).

It is likely that the low diversity and relatively homogenized species composition of the understory, relative to the canopy (Fig. 2, Fig. 4, Fig. 5), is due to the combined effects of fire suppression, pervasive deer browsing, and low-severity disturbance regimes. These three factors all promote the regeneration of shade tolerant species (Abrams and Nowacki 1992) and browse-tolerant species (Banta et al. 2005; Horsley et al. 2003), as well as the exclusion of mid-tolerant and intolerant species. Larger disturbances, with estimated return times of 500-1500 years (Canham and Loucks 1984; Frelich and Lorimer 1991; Seymour et al. 2002), can maintain mid-tolerant and intolerant species (Petraitis et al. 1989). However, recent work has shown idiosyncratic effects of intermediate and large-scale disturbances on regeneration patterns due to variation in disturbance severity, survival rates of canopy trees, availability of propagules, stand history, and biotic interactions such as deer browse (Cooper-Ellis et al. 1999; Peterson and Carson 1996; Peterson and Pickett 1995; Webb and Scanga 2001). Therefore, while it is possible that larger disturbances in the future may promote the regeneration and maintenance of mid-tolerant and shade intolerant species, it is beyond the scope of this study to predict the consequences of such disturbances on the regeneration patterns of these stands.

1.4.3 Implications for conservation and management

The old-growth stands sampled were not undisturbed examples of pre-European temperate forests; it is likely that such forests are exceedingly rare in the eastern USA (Davis 1996). Many of these stands experienced some selective logging (Abrams and Orwig 1996; Orwig and Abrams 1999), loss of chestnut (Aughanbaugh 1935), and possible edge-effects from the clear-cutting of adjacent forests. However, while not pristine, these stands show characteristics (e.g. basal area, coarse woody debris) consistent with values reported for other old-growth stands and which have often been used to define "old-growth" (Keddy and Drummond 1996). Stand basal areas ranged from 12.9 - 83.72 m^2 ha^{-1} (Table 1), comparable to the range of 26 to 61m^2 ha^{-1} found in other eastern old growth stands (Chokkalingam and White 2001; Keddy and Drummond 1996; McGee et al. 1999; Tyrrell and Crow 1994; Ziegler 2000). Additionally, the volume of coarse woody debris ranged from 27.64 - 613.54 m^3 ha^{-1} (Table 1), with most stands consistent with the range of 29 to 180.9 m^3 ha^{-1} found in other eastern old growth stands (Chokkalingam and White 2001; McGee et al. 1999; Ziegler 2000). The HCANF stand had a much higher CWD volume (613.54 m^3 ha^{-1}) than the other 18 stands in this study (Table 1), and higher than the CWD volume found in other eastern old growth stands (Chokkalingam and White 2001; McGee et al. 1999; Ziegler 2000). Beech (*F. grandifolia*) is common in the canopy and subcanopy of HCANF (Fig. 5), and it is likely that the high CWD volume of the HCANF stand is due to beech canopy tree mortality as a result of beech bark disease in this stand, described by Runkle (2007).

Therefore, although these stands are not pristine examples of pre-European forest, they are representative of the known examples of old growth forest in the eastern USA. Old growth stands serve as valuable tools for understanding forest dynamics and determining reference points for the management of future old-growth. However, the conservation and management of existing old growth, and the management of secondary forests for old growth characteristics, requires a better understanding of regeneration patterns of current old-growth stands.

We found common patterns of regeneration across stands, including a lower diversity in the understory than in the canopy, low understory density, and a shift in the understory species composition from that found in the canopy. These patterns of regeneration suggest that fire suppression, deer browsing, and gap-phase dynamics all partly underlie these shifts in understory species composition. In the absence of large-scale disturbances, these shifts in understory species composition are likely to persist, as understory individuals recruit into the canopy.

Furthermore, this shift in understory species composition may cause dramatic changes in future canopy composition if pathogen induced mortality (e.g. hemlock woolly adelgid, beech bark disease, emerald ash borer) increases canopy turn-over in the coming century.

Table 1. Stand names (including abbreviations used in Figures), coordinates, physiographic region, stand type, stand size, percent of the stand sampled, live tree basal area (m^2 ha^{-1}), live tree stem density (stems ha^{-1}), and volume of coarse woody debris (CWD, m^3 ha^{-1}).

Stand Name	Location	Region[a]	Stand Type[b]	Stand Size	% Stand Sampled	Basal Area	Stem Density	CWD
Ander's Run Natural Area (ARNA)	41° 49' 33N, 79° 16' 45W	AP	RO	4.2	12.96	38.91	786.08	104.78
Alan Seeger Natural Area (ASNA)	40° 41' 39N, 79° 16' 45W	RV	RO	20.5	7.97	39.49	408.96	91.31
Bark Cabin Natural Area (BCNA)	41° 25' 09N, 77° 23' 12W	DV	RO	6.5	8.38	12.90	585.88	27.64
Bear Meadows Natural Area (BMNA)	40° 43' 45N, 77° 45' 44W	RV	RO	136	1.33	34.16	563.11	89.39
Bear Run Natural Area (BRNA)	40° 53' 13N, 77° 19' 18W	AP	RO	3.25	16.75	43.43	808.12	86.98
Cranberry Swamp Natural Area (CSNA)	41° 15' 12N, 77° 43' 28W	DV	RO*	52.7	1.38	25.64	611.60	40.29
Cook Trail - Cook Forest (CTCF)	41° 19' 56N, 79° 11' 35W	AP	HE	16.2	9.52	43.14	413.57	145.96
Deer Meadow - Cook Forest (DMCF)	41° 21' 51N, 79° 13' 23W	AP	HE	12.3	7.38	38.89	484.87	166.78
Detweiler Run Natural Area (DRNA)	40° 43' 21N, 77° 44' 18W	RV	RO	28	5.83	37.64	470.18	96.78
Forest Cathedral - Cook Forest (FCCF)	41° 20' 33N, 79° 12' 32W	AP	HE	17.8	8.16	50.22	562.70	144.18
Forrest H. Duttlinger Natural Area (FDNA)	41° 28' 10N, 77° 53' 33W	DV	HE	13.5	5.38	55.81	735.57	84.19
Heart's Content - Allegheny National Forest (HCANF)	41° 41' 24N, 79° 14' 52W	AP	HE	12	9.07	40.74	458.24	613.54
Johnson Run Natural Area (JRNA)	41° 21' 36N, 78° 04' 07W	DV	RO	27.8	4.24	36.46	667.97	46.51
Lower Jerry Run Natural Area (LJRNA)	41° 15' 42N, 78° 04' 07W	DV	RO	2.75	19.80	40.15	383.86	30.90
Swamp Area - Cook Forest (SACF)	41° 23' 36N, 79° 12' 49W	AP	HE$	26	4.19	83.72	1178.20	152.94
Snyder-Middlesworth Natural Area (SMNA)	40° 48' 36N, 77° 17' 13W	RV	HE	10.3	17.62	24.74	547.68	139.64
Seneca Trail - Cook Forest (STCF)	41° 19' 44N, 79° 12' 45W	AP	HE	13.6	6.67	42.62	403.32	312.94
Tionesta - Allegheny National Forest (TANF)	41° 38' 36N, 78° 56' 49W	AP	HE	1267	0.15	27.47	934.58	251.50
Wykoff Run Natural Area WRNA)	41° 14' 46N, 78° 11' 40W	DV	RO	73.7	1.72	31.19	506.91	58.05

a "AP" is High Allegheny Plateau, "DV" is Deep Valley Allegheny Plateau, and "RV" is Ridge and Valley (DCNR 2000)

b "RO" is Hemlock - red oak - mixed hardwood stand type, "HE" is hemlock - white pine - northern hardwood stand type (sensu, Fike 1999)

* CSNA can be more specifically classified as a red oak - mixed hardwood forest type, due to the low representation of conifers (Fike 1999)

$ SACF can be more specifically classified as a hemlock - mixed hardwood palustrine forest, due to the temporal inundation of the stand (Fike 1999)

Table 2. Results of Anova for Shannon diversity index at the stand level and for Tukey's Honestly Significant Difference comparisons between individual size classes. See Table 1 for stand names. Size classes are abbreviated in the Comparisons column as: canopy (CAN), subcanopy (SUB), and understory (UND). Degrees of freedom (d.f.) are shown for class and residuals. Note that p-values > 0.05 are in bold.

Stand	Comparison	d.f.	F value	P value
ARNA	Stand-level	2,15	0.41	**0.99**
	CAN - UND	1,15		**0.99**
	CAN - SUB	1,15		**0.7**
	SUB - UND	1,15		**0.75**
ASNA	Stand-level	2, 51	27.09	< 0.001
	CAN - UND	1, 51		<0.001
	CAN - SUB	1, 51		0.006
	SUB - UND	1, 51		<0.001
BCNA	Stand-level	2, 15	24.16	<0.001
	CAN - UND	1, 15		<0.001
	CAN - SUB	1, 15		0.02
	SUB - UND	1, 15		0.003
BMNA	Stand-level	2, 57	29.18	<0.001
	CAN - UND	1, 57		<0.001
	CAN - SUB	1, 57		<0.001
	SUB - UND	1, 57		0.03
BRNA	Stand-level	2, 15	17.93	<0.001
	CAN - UND	1, 15		<0.001
	CAN - SUB	1, 15		0.01
	SUB - UND	1, 15		**0.052**
CSNA	Stand-level	2, 21	1.22	**0.31**
	CAN - UND	1, 21		**0.38**
	CAN - SUB	1, 21		**0.38**
	SUB - UND	1, 21		**1**
CTCF	Stand-level	2, 39	23.28	<0.001
	CAN - UND	1, 39		<0.001
	CAN - SUB	1, 39		0.042
	SUB - UND	1, 39		<0.001
DMCF	Stand-level	2, 27	16.07	<0.001
	CAN - UND	1, 27		<0.001
	CAN - SUB	1, 27		0.0033
	SUB - UND	1, 27		**0.14**
DRNA	Stand-level	2, 51	17.2	<0.001
	CAN - UND	1, 51		<0.001
	CAN - SUB	1, 51		**0.35**
	SUB - UND	1, 51		<0.001
FCCF	Stand-level	2, 45	25.2	<0.001
	CAN - UND	1, 45		<0.001
	CAN - SUB	1, 45		<0.001
	SUB - UND	1, 45		**0.16**
FDNA	Stand-level	2, 21	7.02	0.0046
	CAN - UND	1, 21		0.0042
	CAN - SUB	1, 21		**0.56**
	SUB - UND	1, 21		0.04
HCANF	Stand-level	2, 33	8.32	0.001
	CAN - UND	1, 33		0.02
	CAN - SUB	1, 33		0.001
	SUB - UND	1, 33		**0.49**
JRNA	Stand-level	2, 36	6.72	0.003
	CAN - UND	1, 36		0.003
	CAN - SUB	1, 36		**0.05**
	SUB - UND	1, 36		**0.46**
LJRNA	Stand-level	2, 15	5.66	0.02
	CAN - UND	1, 15		0.01
	CAN - SUB	1, 15		**0.11**
	SUB - UND	1, 15		**0.49**
SACF	Stand-level	2, 57	41.76	<0.001
	CAN - UND	1, 57		<0.001
	CAN - SUB	1, 57		<0.001
	SUB - UND	1, 57		<0.001
SMNA	Stand-level	2, 33	15.23	<0.001
	CAN - UND	1, 33		<0.001
	CAN - SUB	1, 33		0.02
	SUB - UND	1, 33		0.03
STCF	Stand-level	2, 27	13.81	<0.001
	CAN - UND	1, 27		<0.001
	CAN - SUB	1, 27		0.007
	SUB - UND	1, 27		**0.16**
TANF	Stand-level	2, 60	17.36	<0.001
	CAN - UND	1, 60		<0.001
	CAN - SUB	1, 60		**0.82**
	SUB - UND	1, 60		<0.001
WRNA	Stand-level	2, 39	5.56	0.008
	CAN - UND	1, 39		0.006
	CAN - SUB	1, 39		**0.55**
	SUB - UND	1, 39		0.08

Table 3. Results of Anova for species richness at the stand level and for Tukey's Honestly Significant Difference comparisons between individual size classes. Size classes are abbreviated in the Comparisons column as: canopy (CAN), subcanopy (SUB), and understory (UND). Note that p-values > 0.05 are in bold.

Stand	Comparison	d.f.	F value	P value
ARNA	Stand-level	2,15	0.42	**0.66**
	CAN - UND	1,15		**0.67**
	CAN - SUB	1,15		**0.77**
	SUB - UND	1,15		**0.98**
ASNA	Stand-level	2, 51	38.67	< 0.001
	CAN - UND	1, 51		<0.001
	CAN - SUB	1, 51		<0.001
	SUB - UND	1, 51		<0.001
BCNA	Stand-level	2, 15	36.18	<0.001
	CAN - UND	1, 15		<0.001
	CAN - SUB	1, 15		0.001
	SUB - UND	1, 15		0.003
BMNA	Stand-level	2, 57	21.88	<0.001
	CAN - UND	1, 57		<0.001
	CAN - SUB	1, 57		<0.001
	SUB - UND	1, 57		0.03
BRNA	Stand-level	2, 15	16.47	<0.001
	CAN - UND	1, 15		<0.001
	CAN - SUB	1, 15		**0.97**
	SUB - UND	1, 15		0.007
CSNA	Stand-level	2, 21	4.34	0.03
	CAN - UND	1, 21		0.04
	CAN - SUB	1, 21		**0.97**
	SUB - UND	1, 21		**0.06**
CTCF	Stand-level	2, 39	25.25	<0.001
	CAN - UND	1, 39		<0.001
	CAN - SUB	1, 39		0.002
	SUB - UND	1, 39		0.005
DMCF	Stand-level	2, 27	16.37	<0.001
	CAN - UND	1, 27		<0.001
	CAN - SUB	1, 27		0.01
	SUB - UND	1, 27		0.04
DRNA	Stand-level	2, 51	15.1	<0.001
	CAN - UND	1, 51		<0.001
	CAN - SUB	1, 51		**0.95**
	SUB - UND	1, 51		<0.001
FCCF	Stand-level	2, 45	39.3	<0.001
	CAN - UND	1, 45		<0.001
	CAN - SUB	1, 45		<0.001
	SUB - UND	1, 45		**0.05**
FDNA	Stand-level	2, 21	10.72	<0.001
	CAN - UND	1, 21		<0.001
	CAN - SUB	1, 21		**0.13**
	SUB - UND	1, 21		0.04
HCANF	Stand-level	2, 33	12.91	<0.001
	CAN - UND	1, 33		0.002
	CAN - SUB	1, 33		<0.001
	SUB - UND	1, 33		**0.49**
JRNA	Stand-level	2, 36	10.46	<0.001
	CAN - UND	1, 36		<0.001
	CAN - SUB	1, 36		**0.25**
	SUB - UND	1, 36		0.02
LJRNA	Stand-level	2, 15	17.47	<0.001
	CAN - UND	1, 15		<0.001
	CAN - SUB	1, 15		0.008
	SUB - UND	1, 15		**0.08**
SACF	Stand-level	2, 57	38.91	<0.001
	CAN - UND	1, 57		<0.001
	CAN - SUB	1, 57		<0.001
	SUB - UND	1, 57		<0.001
SMNA	Stand-level	2, 33	4.02	0.03
	CAN - UND	1, 33		0.02
	CAN - SUB	1, 33		**0.55**
	SUB - UND	1, 33		**0.2**
STCF	Stand-level	2, 27	11.93	<0.001
	CAN - UND	1, 27		<0.001
	CAN - SUB	1, 27		0.008
	SUB - UND	1, 27		**0.3**
TANF	Stand-level	2, 60	12.11	<0.001
	CAN - UND	1, 60		<0.001
	CAN - SUB	1, 60		**0.56**
	SUB - UND	1, 60		0.002
WRNA	Stand-level	2, 39	5.15	0.01
	CAN - UND	1, 39		0.009
	CAN - SUB	1, 39		**0.55**
	SUB - UND	1, 39		**0.1**

Table 4. Nonparametric MANOVA results for species composition at stand-level and size class contrasts (1000 permutations for all analyses). See Table 1 for stand names. Plots with no stems in the size classes being compared were removed from analyses, as dissimilarity indices could not be calculated in the absence of stems. Note that p-values > 0.05 are in bold.

Stand	Comparison	F value	P value
ARNA	Stand-level	3.9	<0.01
	CAN - UND	7.4	<.001
	CAN - SUB	2.3	0.05
	SUB - UND	2.6	**0.06**
ASNA	Stand-level	3.0	<0.01
	CAN - UND	4.9	<0.001
	CAN - SUB	5.5	<0.001
	SUB - UND	1.7	**0.08**
BCNA	Stand-level	2.9	<0.01
	CAN - UND	4.2	<0.001
	CAN - SUB	3.0	0.02
	SUB - UND	1.6	**0.18**
BMNA	Stand-level	7.2	<0.01
	CAN - UND	7.3	<0.001
	CAN - SUB	9.9	<0.001
	SUB - UND	5.1	<0.001
BRNA	Stand-level	9.4	<0.01
	CAN - UND	8.6	<0.001
	CAN - SUB	6.5	0.002
	SUB - UND	14.7	<0.001
CSNA	Stand-level	5.4	<0.01
	CAN - UND	8.0	<0.001
	CAN - SUB	5.6	0.002
	SUB - UND	4.8	<0.001
CTCF	Stand-level	5.7	<0.01
	CAN - UND	8.4	<0.001
	CAN - SUB	2.8	0.03
	SUB - UND	4.8	<0.001
DMCF	Stand-level	10.9	<0.01
	CAN - UND	10.5	<0.001
	CAN - SUB	13.4	<0.001
	SUB - UND	9.8	<0.001
DRNA	Stand-level	5.0	<0.01
	CAN - UND	7.7	<0.001
	CAN - SUB	4.0	0.003
	SUB - UND	3.2	0.002
FCCF	Stand-level	5.3	<0.01
	CAN - UND	5.5	<0.001
	CAN - SUB	7.1	<0.001
	SUB - UND	3.7	0.02
FDNA	Stand-level	2.2	0.03
	CAN - UND	3.6	0.01
	CAN - SUB	0.8	**0.51**
	SUB - UND	2.2	**0.10**
HCANF	Stand-level	3.2	<0.01
	CAN - UND	4.8	<0.001
	CAN - SUB	5.7	<0.001
	SUB - UND	0.3	**0.84**
JRNA	Stand-level	3.3	0.01
	CAN - UND	5.7	<0.001
	CAN - SUB	3.8	0.01
	SUB - UND	0.9	**0.37**
LJRNA	Stand-level	4.5	<0.01
	CAN - UND	9.2	<0.001
	CAN - SUB	0.6	**0.52**
	SUB - UND	5.8	<0.001
SACF	Stand-level	6.3	<0.01
	CAN - UND	8.7	<0.001
	CAN - SUB	9.4	<0.001
	SUB - UND	3.4	0.023
SMNA	Stand-level	8.7	<0.01
	CAN - UND	13.3	<0.001
	CAN - SUB	14.5	<0.001
	SUB - UND	1.0	**0.34**
STCF	Stand-level	1.3	**0.20**
	CAN - UND	1.6	**0.14**
	CAN - SUB	0.9	**0.47**
	SUB - UND	0.3	**0.92**
TANF	Stand-level	17.9	<0.01
	CAN - UND	34.7	<0.001
	CAN - SUB	2.1	**0.05**
	SUB - UND	19.0	<0.001
WRNA	Stand-level	6.2	<0.01
	CAN - UND	9.7	<0.001
	CAN - SUB	1.7	**0.11**
	SUB - UND	6.3	<0.001

Table 5. Results of Kruskal-Wallis tests on the relative abundance of oak (Quercus), subdominant mixed hardwood species (HW), hemlock (Tsca), and beech (Fagr) between understory and canopy layers. Not all sites show results for all species because not all species were present at sites, or present in high enough abundance to conduct analyses. Note that p-values > 0.05 are in bold.

Stand	Species	Chi-Squared	P value
ARNA	Quercus	8.6	0.003
ARNA	HW	0.6	**0.42**
ARNA	Tsca	5.3	0.02
ARNA	Fagr	8.6	0.003
ASNA	Quercus	20.6	<0.001
ASNA	HW	8.6	0.003
ASNA	Tsca	0.4	**0.54**
BCNA	Quercus	9.5	0.002
BCNA	HW	6.1	0.01
BCNA	Tsca	0.4	**0.52**
BMNA	Quercus	22.7	<0.001
BMNA	HW	0.2	**0.68**
BMNA	Tsca	0.2	**0.70**
BRNA	Quercus	5.2	0.02
BRNA	HW	4.6	0.03
BRNA	Tsca	8.4	0.004
CSNA	Quercus	12.3	<0.001
CSNA	HW	0.6	**0.44**
CTCF	Quercus	15.2	<0.001
CTCF	HW	0.1	**0.81**
CTCF	Tsca	4.7	0.03
CTCF	Fagr	6.8	0.009
DMCF	HW	5.6	0.02
DMCF	Tsca	12.1	0.001
DMCF	Fagr	8.0	0.005
DRNA	Quercus	11.7	0.001
DRNA	HW	2.9	**0.09**
DRNA	Tsca	9.5	0.002
DRNA	Fagr	1.4	**0.23**
FCCF	HW	10.1	0.002
FCCF	Tsca	21.1	<0.001
FCCF	Fagr	4.6	0.03
FDNA	Tsca	10.6	0.001
HCANF	HW	2.1	**0.15**
HCANF	Tsca	0.0	**0.95**
HCANF	Fagr	6.1	0.01
JRNA	Quercus	17.1	<0.001
JRNA	HW	2.7	**0.10**
JRNA	Tsca	0.0	**0.98**
LJRNA	Quercus	6.2	0.01
LJRNA	Tsca	8.3	0.004
SACF	Quercus	20.9	<0.001
SACF	HW	10.6	0.001
SACF	Tsca	16.3	<0.001
SACF	Fagr	1.3	**0.25**
SMNA	Tsca	14.6	<0.001
STCF	Tsca	0.6	**0.43**
TANF	HW	5.5	0.02
TANF	Tsca	20.4	<0.001
TANF	Fagr	27.0	<0.001
WRNA	Quercus	7.1	0.008
WRNA	HW	2.0	**0.15**
WRNA	Tsca	5.0	0.03

Table 6. Results of Kruskal-Wallis tests on the abundance of shade-tolerant species (sensu, Burns and Honkala 1990) in understory and canopy size classes. Note that p-values > 0.05 are in bold.

Stand	Chi-Square	P value
ARNA	7.4	0.006
ASNA	6.7	0.01
BCNA	8.0	0.005
BMNA	25.2	<0.001
BRNA	8.4	0.004
CSNA	11.7	0.001
CTCF	13.0	<0.001
DMCF	10.8	0.001
DRNA	4.8	0.03
FCCF	19.9	<0.001
FDNA	8.9	0.003
HCANF	4.6	0.03
JRNA	19.0	<0.001
LJRNA	8.3	0.004
SACF	19.8	<0.001
SMNA	10.1	0.001
STCF	0.3	**0.59**
TANF	14.9	<0.001
WRNA	8.7	0.003

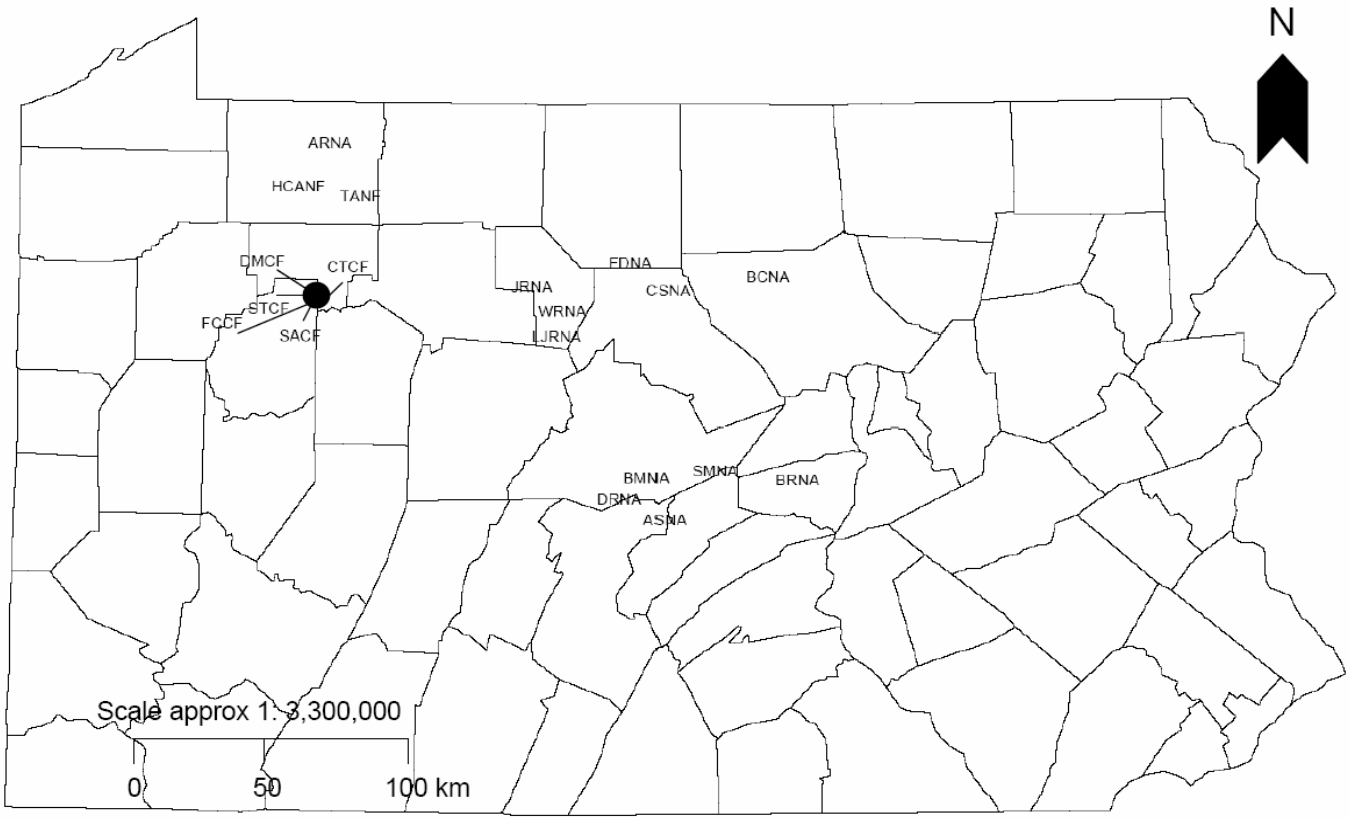

Figure 1. Map of Pennsylvania and positions of the stands sampled. Note that stand locations are not exact in order to clearly identify stand names. See Table 1 for stand names and descriptive information.

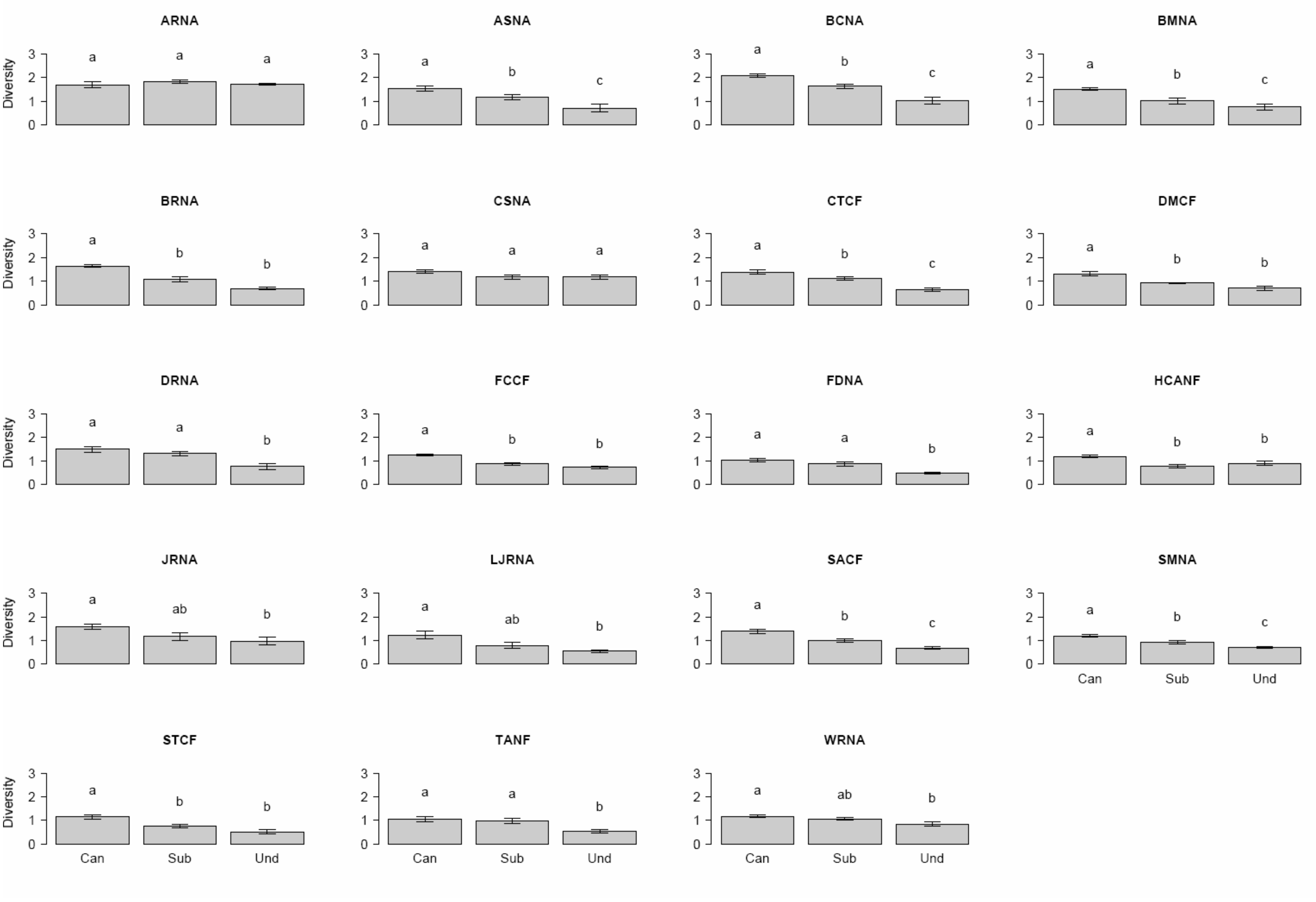
ARNA
ASNA
BCNA
BMNA
BRNA
CSNA
CTCF
DMCF
DRNA
FCCF
FDNA
HCANF
JRNA
LJRNA
SACF
SMNA
STCF
TANF
WRNA
Diversity
0
1
2
3
a
b
c
ab
Can
Sub
Und

Figure 2. Size class Shannon diversity in the canopy (Can: >25cm d.b.h.), subcanopy (Sub: 10 - 25cm d.b.h.), and understory (Und: 0.1 - 10cm d.b.h.) size classes in all 19 stands (see Table 1 for stand names). Results of Tukey's HSD contrasts are shown as letters indicating significant differences.

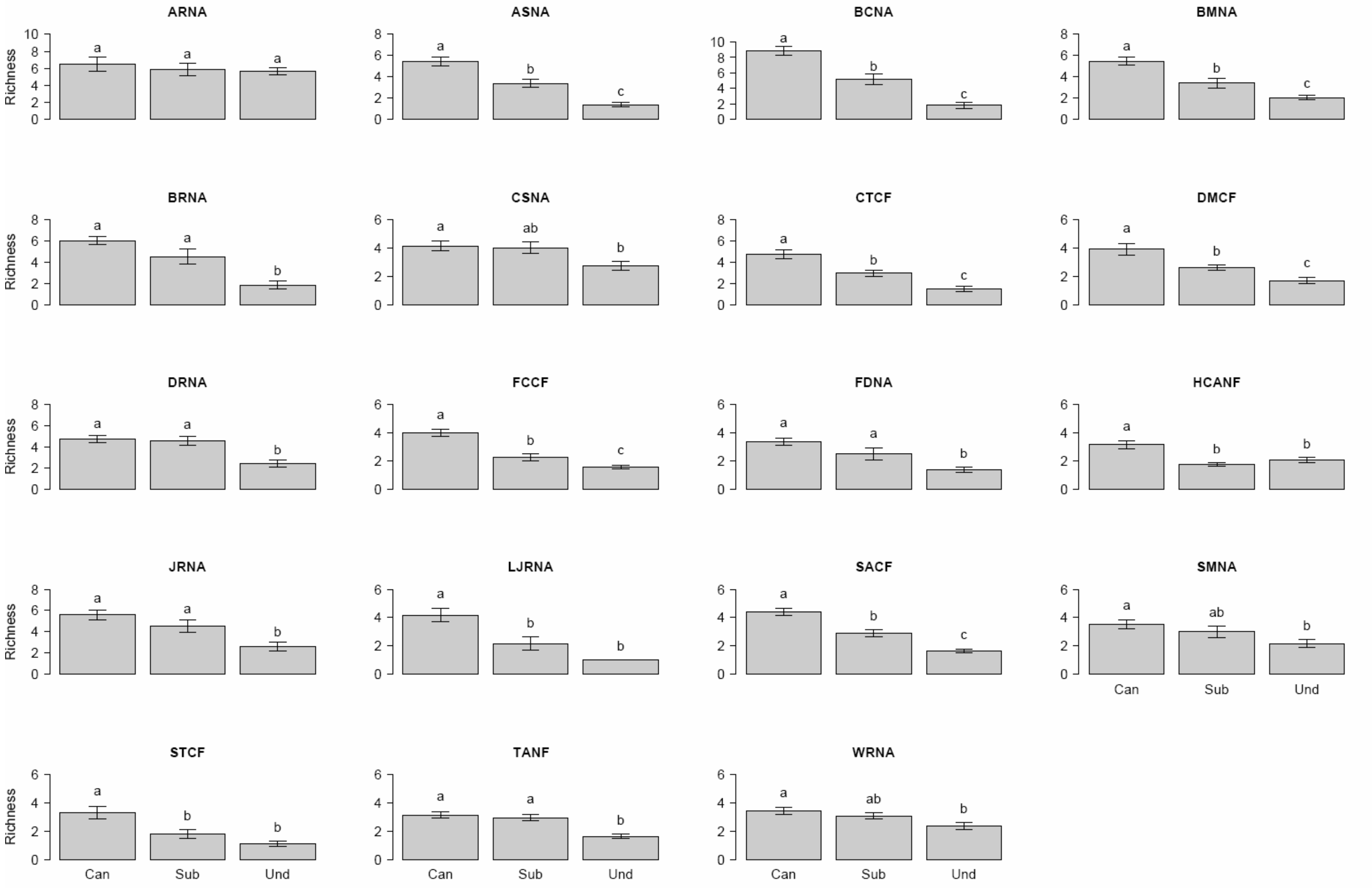
ARNA
ASNA
BCNA
BMNA
BRNA
CSNA
CTCF
DMCF
DRNA
FCCF
FDNA
HCANF
JRNA
LJRNA
SACF
SMNA
STCF
TANF
WRNA
Richness
Can
Sub
Und
a
ab
b
c

Figure 3. Species richness in the canopy (Can), subcanopy (Sub), and understory (Und) size classes in all 19 stands (see Table 1 for stand names). Results of Tukey's HSD contrasts are shown as letters indicating significant differences. Note that the scale of the y-axis differs between stands.

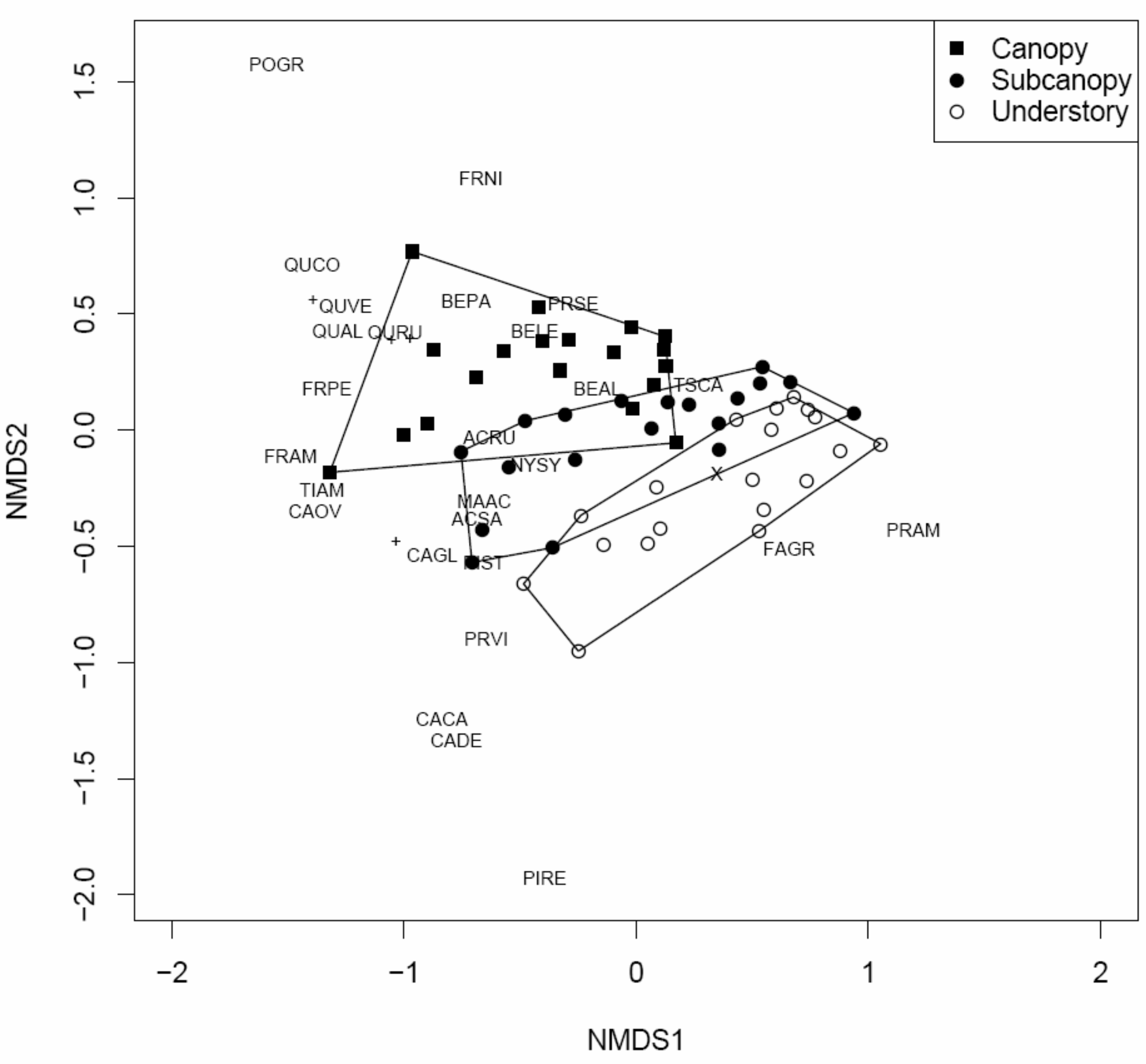
■ Canopy
● Subcanopy
○ Understory
NMDS1
NMDS2
−2
−1
0
1
2
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
POGR
FRNI
QUCO
QUVE
BEPA
PRSE
QUAL
QURU
BELE
FRPE
BEAL
TSCA
ACRU
FRAM
NYSY
TIAM
CAOV
MAAC
ACSA
CAGL
NYSY
PRAM
FAGR
PRVI
CACA
CADE
PIRE
X

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of species abundance in canopy (filled squares, ■), subcanopy (filled circles, ●), and understory (open circles, ○) for each stand. Each symbol represents the canopy, subcanopy, or understory of an individual stand; therefore there are 19 of each symbol. Four letter species name abbreviations indicate the positioning of all species sampled. Key species names are TSCA: *Tsuga canadensis*, ACSA: *Acer saccharum*, FAGR: *Fagus grandifolia*, BEAL: *Betula alleghaniensis*, BELE: *Betula lenta*, QURU: *Quercus rubra*, QUAL: *Quercus alba*. '+' symbols indicate overlapping species names, in which case, the less abundant species name is replaced by '+.'

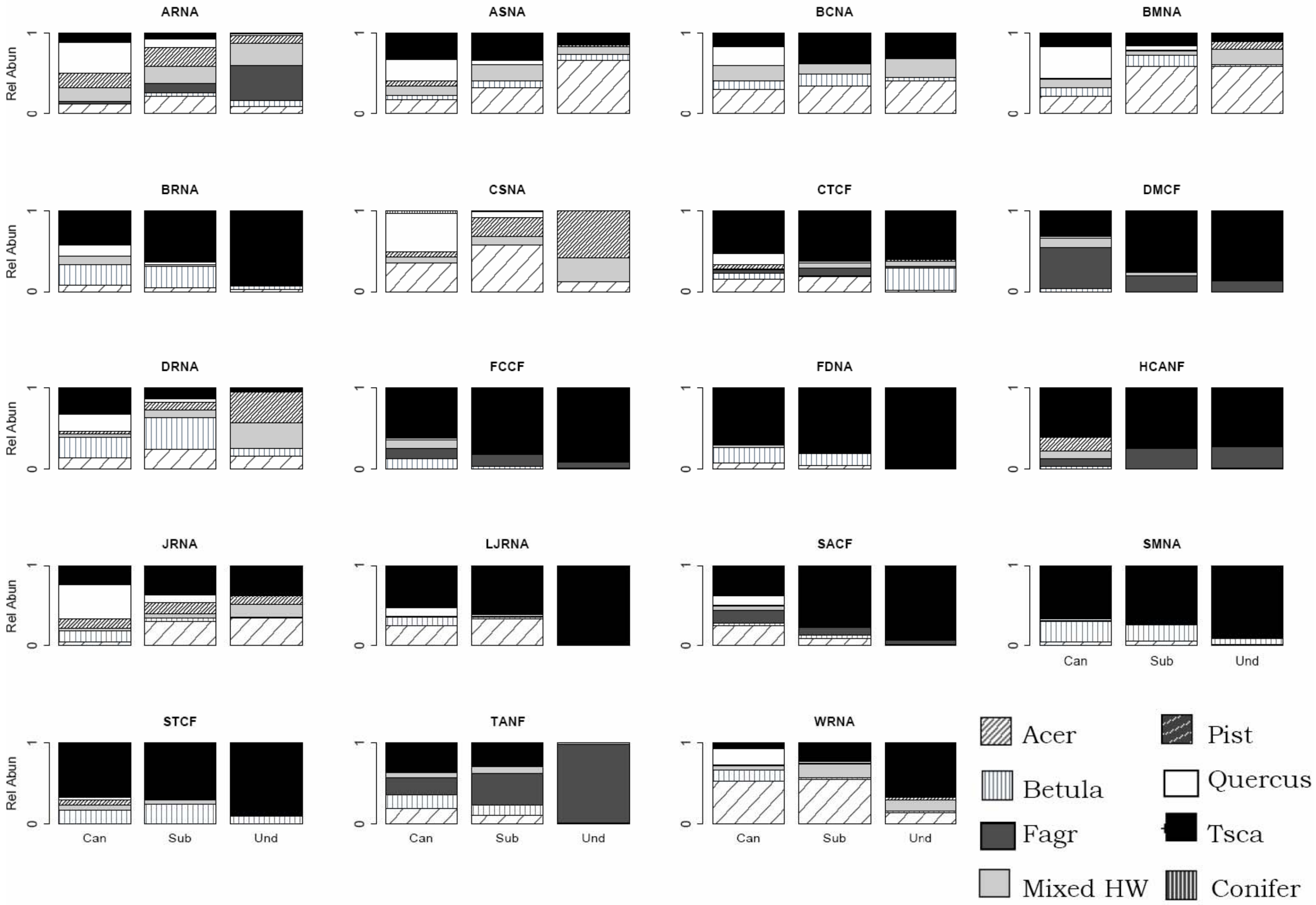
ARNA
ASNA
BCNA
BMNA
BRNA
CSNA
CTCF
DMCF
DRNA
FCCF
FDNA
HCANF
JRNA
LJRNA
SACF
SMNA
STCF
TANF
WRNA
Rel Abun
0
1
Can
Sub
Und
Acer
Pist
Betula
Quercus
Fagr
Tsca
Mixed HW
Conifer

Figure 5. Relative abundance of all species in the canopy (Can), subcanopy (Sub), and understory (Und) size classes in all 19 stands (see Table 1 for stand names). "Mixed hardwood (HW)" category includes all hardwood species comprising less than ten percent of the stems in the stand (e.g. *Liriodendron tulipifera*, *Fraxinus americana*, *Nyssa sylvatica*), while "Conifer" category includes *Picea rubens* and *Pinus resinosa*. *Acer, Betula,* and *Quercus* species are pooled into their respective genera. Species abbreviations: Fagr: *Fagus grandifolia*, Pist: *Pinus strobus*, Tsca: *Tsuga canadensis*.

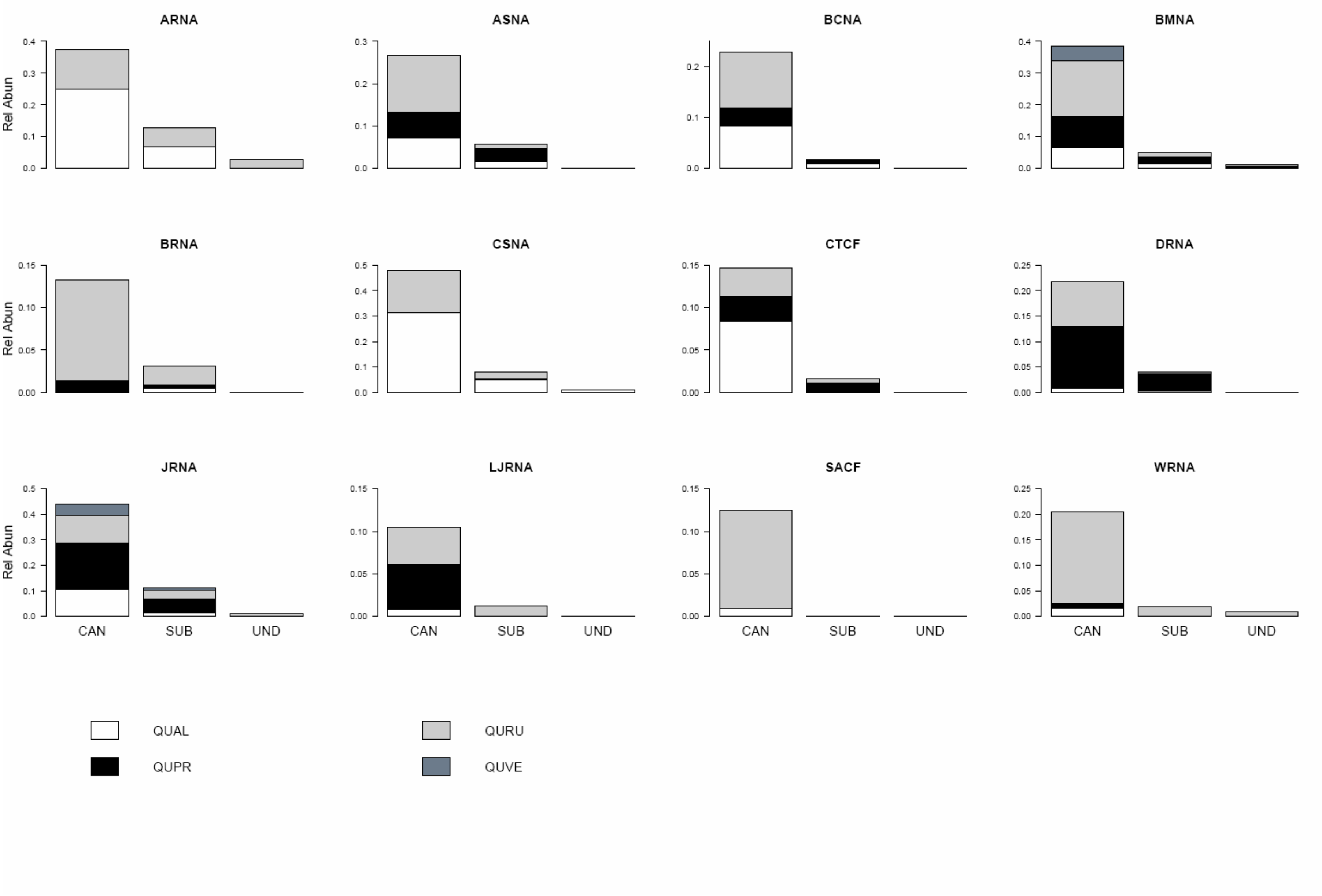
ARNA
ASNA
BCNA
BMNA
BRNA
CSNA
CTCF
DRNA
JRNA
LJRNA
SACF
WRNA
Rel Abun
0.0
0.1
0.2
0.3
0.4
0.5
0.00
0.05
0.10
0.15
0.20
0.25
CAN
SUB
UND
QUAL
QUPR
QURU
QUVE

Figure 6. Relative abundance of *Quercus* species in canopy (Can), subcanopy (Sub), and understory (Und) size classes in 12 stands where pooled relative abundance of *Quercus* species exceeds 10% of canopy. See Table 1 for stand names and Table 5 for results of Kruskal-Wallis tests of difference in abundance between size classes. Species abbreviations: QUAL: *Quercus alba*, QUPR: *Q. prinus*, QURU: *Q. rubra*, QUVE: *Q. velutina*. Note that the scale of the y-axis differs between stands.

APPENDIX

COMPARISON OF SHANNON AND INVERSE SIMPSON'S DIVERSITY INDEX RESULTS

Two diversity indices were used to test for differences in diversity amongst size classes across all stands and within individual stands. There is little consensus in the literature regarding the most appropriate diversity index to use (Jost 2006), therefore, to reduce the likelihood that the choice of the diversity index might bias the results, the Shannon and inverse Simpson's diversity indices were used for all analyses of diversity. The Shannon and inverse Simpson's diversity indices are both commonly used in the literature, however the Shannon diversity weights species equally by their frequency, while the inverse Simpson's diversity disproportionately favors the most common species (Jost 2006). Inverse Simpson's index values were ln transformed to meet the assumptions of ANOVA, though Shannon diversity values did not require transformation for analysis.

The inverse Simpson's diversity index (D) was calculated on a per plot basis as

$$[\mathrm{A1}] \quad D = 1 \Big/ \sum_{i=1}^{S} p_i^2$$

, where S is the total number of species in the plot and p_i is the relative abundance of the i^{th} species (Jost 2006). The results of the ANOVA at the stand level were consistent between the Shannon and inverse Simpson's diversity indices. Specifically, there was a significant difference in diversity between size classes in 17 of 19 stands and this is seen in both the Shannon and inverse Simpson's diversity indices (Stand-level comparisons, Table A1). The ARNA and CSNA stands showed no significant difference in diversity between size classes, and again, this is seen in both the Shannon and inverse Simpson's diversity indices (Stand-level comparisons, Table A1). The results of the Tukey's honestly significant difference contrasts show less consistency between the two diversity indices used, however, qualitatively similar results were found for 18 of 19 contrasts between the understory and canopy size classes (HCANF showed the only inconsistent result between the two diversity indices), and in 47 of the total 57 contrasts (Table A1). The primary focus of these analyses is the comparison of the understory and canopy size classes (see predictions in INTRODUCTION, p. 3), which showed very consistent results irrespective of the diversity index used. Therefore, given the consistency of the results for inverse Simpson's and Shannon index, we only present results for the Shannon's diversity index.

Table A1. Comparisons of the results from Anova for Shannon and Inverse Simpson's (InvSimp) diversity indices at the stand level and for Tukey's Honestly Significant Difference comparisons between individual size classes.

Stand	Comparison		Shannon Diversity		InvSimp Diversity	
		d.f.	F value	P value	F value	P value
ARNA	Stand-level	2,15	0.4	0.99	2.2	0.14
	CAN - UND	1,15		0.99		0.73
	CAN - SUB	1,15		0.7		0.41
	SUB - UND	1,15		0.75		0.13
ASNA	Stand-level	2, 51	27.1	< 0.001	21.0	<0.001
	CAN - UND	1, 51		<0.001		<0.001
	CAN - SUB	1, 51		0.006		0.003
	SUB - UND	1, 51		<0.001		0.011
BCNA	Stand-level	2, 15	24.2	<0.001	20.3	<0.001
	CAN - UND	1, 15		<0.001		<0.001
	CAN - SUB	1, 15		0.02		0.004
	SUB - UND	1, 15		**0.003**		**0.076**
BMNA	Stand-level	2, 57	29.2	<0.001	24.8	<0.001
	CAN - UND	1, 57		<0.001		<0.001
	CAN - SUB	1, 57		<0.001		<0.001
	SUB - UND	1, 57		**0.03**		**0.1**
BRNA	Stand-level	2, 15	17.9	<0.001	10.7	0.001
	CAN - UND	1, 15		<0.001		0.001
	CAN - SUB	1, 15		0.01		0.013
	SUB - UND	1, 15		0.05		0.49
CSNA	Stand-level	2, 21	1.2	0.31	0.9	0.41
	CAN - UND	1, 21		0.38		0.48
	CAN - SUB	1, 21		0.38		0.48
	SUB - UND	1, 21		1		1
CTCF	Stand-level	2, 39	23.3	<0.001	15.0	<0.001
	CAN - UND	1, 39		<0.001		<0.001
	CAN - SUB	1, 39		**0.04**		**0.15**
	SUB - UND	1, 39		<0.001		0.003
DMCF	Stand-level	2, 27	16.1	<0.001	16.3	<0.001
	CAN - UND	1, 27		<0.001		<0.001
	CAN - SUB	1, 27		0.003		<0.001
	SUB - UND	1, 27		0.14		0.70
DRNA	Stand-level	2, 51	17.2	<0.001	13.8	<0.001
	CAN - UND	1, 51		<0.001		<0.001
	CAN - SUB	1, 51		0.35		0.13
	SUB - UND	1, 51		<0.001		0.006
FCCF	Stand-level	2, 45	25.2	<0.001	13.3	<0.001
	CAN - UND	1, 45		<0.001		0.002
	CAN - SUB	1, 45		**<0.001**		**0.41**
	SUB - UND	1, 45		**0.16**		**0.04**
FDNA	Stand-level	2, 21	7.0	0.005	3.8	0.034
	CAN - UND	1, 21		0.004		0.035
	CAN - SUB	1, 21		0.56		0.67
	SUB - UND	1, 21		**0.04**		**0.19**
HCANF	Stand-level	2, 33	8.3	0.001	6.4	0.004
	CAN - UND	1, 33		**0.02**		**0.07**
	CAN - SUB	1, 33		0.001		0.004
	SUB - UND	1, 33		0.49		0.44
JRNA	Stand-level	2, 36	6.7	0.003	5.9	0.006
	CAN - UND	1, 36		0.003		0.007
	CAN - SUB	1, 36		**0.05**		**0.04**
	SUB - UND	1, 36		**0.46**		**0.76**
LJRNA	Stand-level	2, 15	5.7	0.02	4.2	0.04
	CAN - UND	1, 15		0.01		0.04
	CAN - SUB	1, 15		0.11		0.097
	SUB - UND	1, 15		0.49		0.87
SACF	Stand-level	2, 57	41.8	<0.001	36.7	<0.001
	CAN - UND	1, 57		<0.001		<0.001
	CAN - SUB	1, 57		<0.001		<0.001
	SUB - UND	1, 57		<0.001		0.05
SMNA	Stand-level	2, 33	15.2	<0.001	15.0	<0.001
	CAN - UND	1, 33		<0.001		<0.001
	CAN - SUB	1, 33		0.02		0.02
	SUB - UND	1, 33		0.03		0.05
STCF	Stand-level	2, 27	13.8	<0.001	11.1	<0.001
	CAN - UND	1, 27		<0.001		<0.001
	CAN - SUB	1, 27		0.007		0.007
	SUB - UND	1, 27		**0.16**		**0.42**
TANF	Stand-level	2, 60	17.4	<0.001	11.9	<0.001
	CAN - UND	1, 60		<0.001		<0.001
	CAN - SUB	1, 60		0.82		0.99
	SUB - UND	1, 60		<0.001		<0.001
WRNA	Stand-level	2, 39	5.6	0.008	4.0	0.03
	CAN - UND	1, 39		0.006		0.02
	CAN - SUB	1, 39		0.55		0.44
	SUB - UND	1, 39		0.08		0.27

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