ECOTONAL CHANGE IN HIGH-ELEVATION FORESTS OF THE GREAT SMOKY

MOUNTAINS, 1930S-2004

by

JULIE PAIGE TUTTLE

(Under the Direction of ALBERT J. PARKER)

ABSTRACT

Recent theory asserts that montane vegetation ecotones may be good locations for observing change because of their association with steep environmental and climatic gradients. In 2004, I sampled the Great Smoky Mountains spruce-fir ecotone for comparison to Frank Miller's 1930s data to examine changes in ecotonal forest composition and structure. Changes in stand attributes as well as shifts in dominant and subdominant species reflect primarily the decimation of *Abies fraseri* by the balsam woolly adelgid and high mortality of *Fagus grandifolia* from beech bark disease. Based on the results of this study, the abundance and distribution of *Picea rubens* seem preserved in the ecotone, pending future recruitment success. *Abies fraseri* persists in a diminished state at the highest elevations. It is unknown whether *Betula lutea* will persist in dominating former *A. fraseri* forests, particularly on north-facing slopes.

INDEX WORDS: spruce-fir, montane ecotone, Great Smoky Mountains, *Picea rubens*, *Abies fraseri*, balsam woolly adelgid, global change, forest disturbance

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DEDICATION

To Carolyn and Sam Donald

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Chapter 1: Introduction

Great Smoky Mountains National Park (GRSM) is prized for its biodiversity and represents one of the largest expanses of protected forest in the eastern United States (211,041 ha). While creation of the park in 1934 ended human settlement, livestock grazing, logging, and post-logging fires within park boundaries, other anthropogenic impacts transgress geographic boundaries and continue to impose change on the forests of the Great Smoky Mountains. Recent and potential future threats to GRSM forests include exotic pest introduction, atmospheric deposition, altered disturbance regimes, and climate change, all of which affect forest composition and structure.

In particular, GRSM's high-elevation spruce-fir forests, thought to be glacial relicts (White and Cogbill 1992), have been exposed to multiple anthropogenic stressors, including extensive pre-park logging of red spruce (*Picea rubens*) (Pyle 1988), decimation of Fraser fir (*Abies fraseri*) by the non-native balsam woolly adelgid (*Adelges piceae* Ratz.) (Smith and Nicholas 1998), and increased stress on *P. rubens* from atmospheric deposition associated with anthropogenic atmospheric inputs (McLaughlin et al. 1993), such as nitric oxides, sulfur dioxide, and ozone. These high-elevation forests contribute to the biodiversity of GRSM; for example, *A. fraseri* is endemic to the southern Appalachian Mountains, and spruce-fir forests provide habitat for species such as the endangered spruce-fir moss spider (*Microhexura montivaga*) (Keith Langdon, personal communication 2004). Consequently, ecological monitoring and analysis of GRSM and other southern Appalachian spruce-fir forests have been ongoing for several decades.

While the study of spruce-fir forests has yielded valuable insight into their response to the range of anthropogenic inputs, most studies have been focused within areas dominated by *P. rubens* and *A. fraseri* (White and Busing 1993). Recent theory, however, asserts that vegetation ecotones, the transition zone between different vegetation types, may be important indicators of change, because species are at their environmental or competitive limits (Gosz 1992, Noble 1993) at these locations. Montane vegetation ecotones in particular, because of their association with steep environmental and climatic gradients, may be good locations for observing change (Beniston 1994). Indeed, paleoecological studies suggest that migration of montane ecotones occurs with changes such as climate warming or altered disturbance regimes (Delcourt and Delcourt 1998). Ecotonal change at observable human time scales may not manifest as a clear shift in vegetation boundaries, especially where vegetation transitions are not abrupt; rather, compositional shifts within or on either side of an ecotone may be the most evident change (Payette et al. 2001). Regardless, ecotonal studies over recent decades have contributed to an understanding of forest dynamics and change.

The lower boundary of GRSM spruce-fir forests represents both a montane deciduous-coniferous ecotone and the lower latitudinal extent of postglacial remnant "boreal" forest in eastern North America (White and Cogbill 1992), making its dynamics of interest in the study of anthropogenic forest change. In addition, rapid regeneration of *A. fraseri* after balsam woolly adelgid infestation (Busing et al. 1988, personal observation 2004) and lower mortality of southern, as compared with northern, *P. rubens* populations from atmospheric deposition (Peart et al. 1992) may combine with other factors (e.g., long lifespan or adaptation to site exposure) to enable persistence of high-elevation *P. rubens*- and *A. fraseri*-dominated forests in spite of such impacts, perhaps supporting the relevance of investigating the deciduous-coniferous ecotone as a

more sensitive indicator of change. Few studies exist, however, focused on montane deciduous-coniferous ecotones in general (Kupfer and Cairns 1996) and the GRSM deciduous-coniferous ecotone in particular (White and Busing 1993).

While multiple field vegetation surveys have been conducted in GRSM – most notably those by Cain (1935), Oosting and Billings (1951), Whittaker (1956), and Golden (1981) – the most comprehensive field survey of GRSM vegetation was conducted by Frank Miller in 1935-1938 (MacKenzie and White 1998). Miller's inclusion of over 133 plots spanning the spruce-fir zone and its ecotone with lower-elevation, primarily northern hardwood forests (Busing et al. 1993) offers an opportunity for analysis of ecotonal change over several decades. Busing et al. (1993) analyzed the Miller ecotonal data, but such a comparison with the present-day ecotone has not been conducted. In 2004, therefore, I sampled the GRSM deciduous-coniferous ecotone for comparison to the Miller data to examine changes in ecotonal forest composition and structure over nearly 70 years.

It should be noted that several factors complicate any study of ecotones and of montane ecotones in particular. The universal value of vegetation ecotones as indicators of both natural and anthropogenic change remains indeterminate; results of studies and models have been site, situation, and time specific. Some studies reveal rapid shifts or changes in ecotones (Allen and Breshears 1998) and others remain inconclusive (Masek 2001). Similar biome transitions in different geographic contexts may exhibit directionally opposite shifts in response to similar inputs, such as fire suppression (Grau and Veblen 2000). Time lags related to such factors as the persistence of established, long-lived trees (e.g., *P. rubens*) and vegetation-reinforced soil gradients (e.g., acidity) may prevent compositional change in temporal step with inputs (White and Cogbill 1992, Malanson 1999). Several factors make causal attribution and modeling or

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prediction of ecotonal change difficult: multiple interactive causes of change across spatial and temporal scales (Hofgaard 1997); feedbacks that enhance or mitigate vegetation responses (Malanson 1999); and individualistic species behavior (White and Cogbill 1992, Woodward 1993). The study of montane ecotones is complicated further by the influence of complex topographic gradients, including slope aspect, steepness, configuration, and position, on vegetation composition (Parker 1982, Welch et al. 2002).

   The above challenges notwithstanding, this study has two objectives: 1) detection of change (or lack of change) in the deciduous-coniferous ecotone of GRSM and 2) examination of composition-topography relationships within this montane ecotone. To this end, I address the following questions: 1) Have forest stand attributes (basal area, density, and diversity) or species composition and abundance in the ecotone changed since the 1930s? 2) Has stand or species size-class structure changed?) 3) Have stand attributes or species composition and abundance changed by elevation within the ecotone? 4) Have ecotone community types and gradients changed? 5) Have compositional relationships to topographic variables changed for the ecotone?

Chapter 2: Study Area

Great Smoky Mountains National Park (35˚ 41' N, 83˚ 32' W) contains the largest remaining tract of undisturbed spruce-fir forest in the southern Appalachians (48% of original area), occurring from approximately 1500 m up to 2025 m at Clingmans Dome (White and Cogbill 1992) and surrounded mostly by northern hardwood forest at its lower boundary (Figure 1). This lower boundary has been related to a mean July temperature of 17˚ C; a hypothesized relationship with frequency of cloud immersion; and increased precipitation with elevation, ranging from 180 to 250 cm per year in the southern Appalachian spruce-fir zone (White and Cogbill 1992). The dominants of southern Appalachian spruce-fir forests, red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*), exhibit individualistic behavior, however. While *A. fraseri* rarely occurs below 1372 m in the southern Appalachians (Burns and Honkala 1990), *P. rubens* may occur with hardwoods and Eastern hemlock (*Tsuga canadensis*) as low as, and perhaps below, 1200 m in GRSM according to a recent remote sensing-based classification (Madden et al. 2004), although the accuracy assessment of this classification has not yet been completed. However, as a result of the frequent occurrence of *P. rubens* at lower elevations than *A. fraseri*, the deciduous-coniferous ecotone in GRSM largely involves *P. rubens*.

Bedrock in GRSM comprises primarily the Thunderhead and Anakeesta formations, metamorphosed sedimentary rock of the late Precambrian era (Moore 1988). Soils of the spruce-fir zone are shallow, acidic Inceptisols or Spodosols (Burns and Honkala 1990). With decreasing elevation and slope steepness, soils generally become deeper and less acidic (Fernandez 1992).
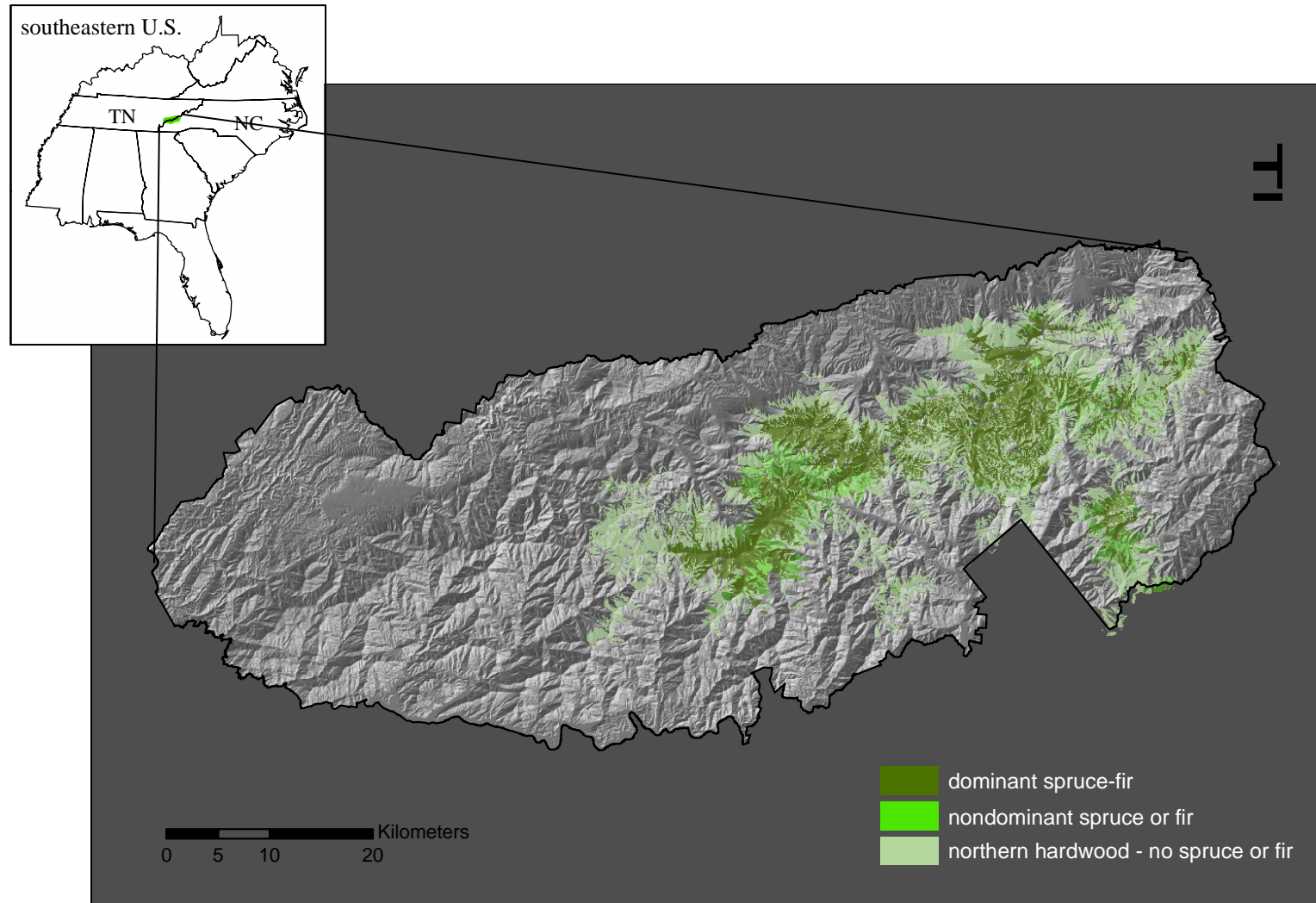
Figure 1. Study area: the spruce-fir zone and its ecotone with northern hardwood forests in Great Smoky Mountains National Park. The map was created in ESRI ArcMap 8.1 using the CRMS vegetation classification data (Madden et al. 2004), a USGS 30-m DEM, and the National Park Service's GRSM boundary shapefile.

Chapter 3: Methods

   Busing et al. (1993) identified 133 undisturbed Miller plots in 13 watersheds containing any

Picea rubens or *Abies fraseri* >4 in. diameter at breast height (dbh). Results of their analysis

suggest a topographically complex, gradual ecotone from primarily northern hardwood to

spruce-fir forest between 1300 and 1600 m elevation. My approach in this study is therefore to

assess change in forest composition and structure *within* this gradual ecotone, across the range of

topographic settings present. Uncertainty in the Miller plot locations makes relocation for direct

resampling difficult and the results of any subsequent paired analysis questionable; consequently,

I collected an independent sample of ecotone plots for comparison to a topographically similar

subset of Miller ecotone plots.

   Botanical nomenclature follows Weakley (2007).

   Miller data.   The Miller field crews sampled park vegetation in a fairly regular grid of 1 x 2-

chain (20 x 40-m) plots across the entire park, with only a few areas sparsely sampled. In each

plot, all trees >4 in. (10.1 cm) dbh were identified to species and tallied in four diameter classes:

4-<12 in. (10.1-30.3 cm), 12-<24 in. (30.4-60.8 cm), 24-<36 in. (60.9-90.3 cm), and ≥36 in.

(>90.3 cm). Environmental data recorded for each plot include elevation (ft), slope steepness

(%), slope aspect (SW, S, W, SE, NW, E, N, and NE), soil depth and texture, litter depth, and

year of most recent logging or fire. The dominant species in the shrub/sapling layer was

recorded for each of 100 contiguous, 2 x 2-m subsections within a ½ x 2-chain (10 x 40-m)

subplot. Each plot location was marked with an X and an alphanumeric label on early

topographic maps. The Uplands Field Research Laboratory (UFRL) of GRSM created digital

files of the Miller vegetation and environmental data from the original data sheets and transferred the plot X locations to modern 1:24,000 scale USGS topographic quadrangle maps, based on the early maps and descriptions of plot location on the data sheets (Busing et al. 1993). Both inaccuracies in the early topographic maps and the lack of modern GPS technology contribute to locational uncertainty for the Miller plots; plot locations as transferred to the modern topographic maps are thought to be accurate to within approximately 50 m (Peter White, personal communication 2004).

Field data collection. Field sampling was designed 1) to represent the geographic extent of the spruce-fir zone in the park, 2) to "bracket" the presumed 1300-1600-m altitudinal range of the northern hardwood and spruce-fir ecotone, and 3) to encompass the range of site types. Five watersheds spanning the spruce-fir zone were selected to maximize the number of undisturbed Miller ecotone plots for comparison, the overall quantity of remaining old-growth forest, and site accessibility. Busing et al. (1993) tallied by watershed the number of undisturbed Miller ecotone plots, and Pyle (1988) compiled historical data to estimate the percentage of remaining old-growth forest in each watershed. Preliminary site accessibility was evaluated considering location of roads and trails on the GRSM park map, inspection of elevation and terrain on USGS topographic quadrangle maps, and insights from field reconnaissance. Field sampling included sites between 1200 and 1700 m, stratified in each watershed by five 100-m elevation zones and eight aspect classes.

Accessible sites were defined and located more specifically during the site selection process. Preliminary site selection was accomplished by geographic information systems (GIS) analysis using 1) a digital map of GRSM vegetation, based on manual interpretation of 1997-98 1:12,000-scale color infrared aerial photography and recently completed by the University of Georgia's

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Center for Remote Sensing and Mapping Science (CRMS) as part of a cooperative agreement with the National Park Service (NPS) (Madden et al. 2004); 2) a USGS 10-m digital elevation model (DEM) of the park, provided by the Plant Ecology Lab at the University of North Carolina; and 3) USGS digital line graph (DLG) roads, trails, and watersheds for GRSM, provided by the park via CRMS. The sampling universe was created by selecting all vegetation between 1200 and 1700 m that was classified by CRMS as dominated or codominated by northern hardwoods/*Tsuga canadensis*, *Picea rubens*, or *P. rubens-Abies fraseri*. Slope steepness and aspect were calculated from the DEM. To accommodate time and labor constraints, sites within 150 m of a trail or road and with slope steepness less than or equal to 60% were selected from this sampling universe. Field reconnaissance also revealed that reasonable access to many sites was obstructed by a dense understory of *Rhododendron* species, so sites mapped by CRMS as dominated or codominated by *Rhododendron* spp. or *Kalmia* sp. were excluded. The resultant map of accessible sites was classified by elevation and aspect, and random locations satisfying the stratification scheme were extracted. Final site selection in the field was modified from these locations according to actual accessibility, topographic homogeneity for a plot size of at least 30 x 60 m, and freedom from recent gross disturbance. Thirty-four sites were sampled.

  At each site, stratified systematic unaligned sampling was used to establish eight non-overlapping, circular 100-m^2 subplots within a 30 x 60-m rectangular plot, pooled to yield a total area sampled of 800 m^2 per plot, equal to Miller plot area. In each subplot, species and dbh (1.4 m) were recorded for all trees ≥10 cm in diameter. Saplings were tallied by species in small (>0 and <5 cm) and large (≥5 and <10 cm) diameter classes within eight nested, circular 50-m^2 subplots. At each plot center, elevation (m), slope steepness (%), slope aspect (°), relative slope

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position (lower, middle, or upper), cross-slope and down-slope configuration (concave, convex, or straight), and GPS coordinates (UTM 17N, NAD27) were recorded. Qualitative site information was noted, such as presence of common understory shrub and herbaceous species, evidence of disturbance, abundance of downed logs, and obvious tree damage by disease or insects.

   Data preparation.   Data preparation included GIS selection in ArcMap 8.1 (Environmental Systems Research Institute, Inc.) of an appropriate subset of Miller plots for comparison to the Tuttle field sample as well as conversion of vegetation and environmental variables in the two data sets to comparable units or classes. The locations of all Miller plots within the five sampled watersheds were manually digitized in UTM/NAD27 coordinates from their locations on the modern topographic quadrangle maps. Plot environmental data were appended to the coordinates. Using ArcMap,, the Miller plot locations were overlaid on USGS digital raster graphics (DRGs) of the 1:24000 scale USGS topographic quadrangle maps, and DEM-derived elevation, aspect, and slope were appended to the plot data to confirm the relative accuracy of the digitized plot locations. Undisturbed Miller plots (no recorded date of logging or burning) that fell within my vegetation sampling universe were selected. Because of the inherent locational uncertainty in plot locations, Miller's elevation, aspect, and slope values – not the DEM-derived values – were used for the Miller data in all subsequent analyses. Thirty-two plots matching the Tuttle elevation-aspect class combinations and with less than 50% cover by *Rhododendron* or *Kalmia* spp. were identified and selected to represent the comparison data set.

   MacKenzie and White (1998) calculated Miller plot basal area (m^2/ha) and density (stems/ha) by species, and Busing et al. (1993) coded aspect classes from high to low relative solar radiation load (SW=1, S=2, W=3, SE=4, NW=5, E=6, N=7, and NE=8). Basal area was calculated by

MacKenzie and White (1998) as the number of stems times basal area for the geometric mean of each size class, summed across all four size classes and converted to meters squared per hectare. For the Tuttle data, each plot's basal area and density by species were calculated from the actual measured values. Miller elevations were converted from feet to meters, and Tuttle aspect values were coded to match Busing et al.'s (1993) classes. In preparation for size-class analysis, trees in the Tuttle data were tallied by species in the same diameter classes as the Miller data. Relative importance value (IV), defined as the sum of relative basal area and relative density, was calculated by species for each Miller and Tuttle plot. The topographic convergence index (TCI), calculated for GRSM and provided by Jobe (2006), was extracted by GIS for all plot locations and was included with elevation, aspect, and slope steepness as a topographic variable in all subsequent analyses. TCI represents the impact of relative slope position and configuration on site potential moisture availability, as a function of upslope drainage area (a) and local slope steepness (tanß) (TCI = ln(a/tanß)) (Beven and Kirkby 1979). Along with elevation, aspect, and slope steepness, TCI has been related to vegetation composition gradients (Urban 2000).

   Analysis.   Basal area and stem density were summarized for each data set by plot and by species. Importance value (IV) and frequency of occurrence (%) additionally were summarized by species. Species richness, species evenness, and Shannon's diversity index were computed for each plot. Differences in stand attributes were assessed using Student's t-test to compare Miller and Tuttle mean plot basal area, density, species richness, species evenness, and Shannon's diversity index. Benjamini and Hochberg's method was used to control the false discovery rate, or the expected proportion of rejected null hypotheses that are erroneously rejected in the setting of multiple significance tests (Benjamini and Hochberg 1995). Differences in species composition and abundance between the two data sets were assessed by visual

comparison of species' mean basal area, density, IV, and frequency of occurrence. Graphs of mean stem density by size class for Miller versus Tuttle stands and species were compared to ascertain differences in size-class structure. To examine stand differences within the ecotone, mean plot basal area and stem density by elevation zone were calculated and compared. Likewise, mean plot basal area, density, and IV were calculated for each species by elevation zone, enabling assessment of 1) how dominant species differ by elevation between the two data sets, 2) which species drive overall stand differences by elevation, and 3) trends in species dominance with elevation, particularly from northern hardwood species to *Picea rubens* and/or *Abies fraseri*.

Plots were grouped into community types for each data set separately with hierarchical, agglomerative cluster analysis of composition by basal area using Ward's linkage method and relative Euclidean distance as the measure of (dis)similarity between plots. Cluster analysis also was performed on the combined Miller and Tuttle data to evaluate overlap or separation of community types in the two data sets. After testing several linkage methods and distance measures, the combination of Ward's method and relative Euclidean distance was chosen because it yielded minimal chaining and ecologically interpretable clusters that were useful for visual interpretation of subsequent analyses. Ward's method, which minimizes the total error sum of squares based on Euclidean distance of plots from cluster centroids (Ward 1963), generally performs well with ecological data (Kent and Coker 1992), and relative Euclidean distance relativizes abundance within plots, minimizing differences based solely on plot total basal area. It should be noted that Sorensen distance, a commonly used distance measure that also performs well with ecological community data (Faith et al. 1987), was not used because it is incompatible with Ward's method (McCune and Mefford 1999). For each of the three cluster

analyses, the final number of clusters was selected to minimize the objective function while maximizing ecological interpretability in the context of this study.

Patterns of species composition were educed using nonmetric multidimensional scaling (NMS) (Kruskal 1964), a distance-based ordination method for indirect gradient analysis. The advantages and disadvantages of NMS versus detrended correspondence analysis (DCA), an eigenanalysis-based ordination method, continue to be debated in the community ecology literature (Faith et al. 1987, Holland and Patzkowsky 2006). After using both methods with the Miller and Tuttle data, I chose NMS using raw basal area for ease of interpretability. Unlike the eigenanalysis-based methods, the number of axes for NMS is user defined, and the axes are not necessarily in order of variance explained. The best solution should minimize "stress", the residual sum of squares between dissimilarity in the original data matrix and distance in ordination space, for a given number of axes and should be stable within the final iterations (standard deviation in stress <0.00001) (McCune and Mefford 1999). I used PC-ORD for Windows 4.37 (McCune and Mefford 1999) in autopilot mode to find the dimensionality with the best solution and to run Monte Carlo randomization tests of significance for stress in the final solution. Using the Sorensen distance measure (McCune and Mefford 1999), NMS ordination of the combined Miller and Tuttle data sets was performed to compare the range of variability present in the data sets and to visualize differences between Miller and Tuttle clusters in ordination space. A separate NMS then was performed for each of the two data sets to assess their community gradients independently. Correlations were performed between topographic variables and NMS axis scores as well as between species abundances and axis scores.

To evaluate and compare compositional and species relationships to topography more directly, canonical correspondence analysis (CCA) (ter Braak 1987) was performed on each data set

separately. CCA is considered direct gradient analysis because the ordination is constrained to a

linear regression of environmental variables on plot species composition. The user must choose

environmental variables with hypothesized relationships to composition; I used four topographic

variables – elevation, slope aspect, slope steepness, and TCI – as proxies for temperature,

precipitation, potential solar radiation, potential heat load, local site drainage, topographic

position, and site potential moisture availability. Monte Carlo tests of significance were

performed for the species-environment correlation and eigenvalue of the first ordination axis.

Chapter 4: Results

Thirty-two unlogged Miller plots met the elevation, aspect, and rhododendron understory criteria to match the 34 Tuttle plots in the five study area watersheds (Figure 2). The plots generally cover the same range of topographic and environmental setting (Table 1). The Tuttle plots range slightly lower in elevation. Because no west-facing plots are included in the Tuttle plots, these are also excluded from the Miller plots. The Miller plots include some steeper slopes than the Tuttle plots. The Tuttle plots encompass a slightly wider range of topographic convergence index (TCI) values than the Miller plots.

When plot locations are overlaid on the park's logging history map (Pyle 1984, Kunze 2003), one Miller plot and six Tuttle plots are located in areas mapped as heavily logged prior to park formation (i.e., in the 1920s). However, this map is an approximation constructed from multiple historical data types, including primarily the Miller data (the locations of which are also approximate). Miller's field crews recorded last year of logging, and the Miller plot location mapped as heavily logged was recorded as unlogged. The species composition and total basal area of this plot indicate that if logged, it was several decades earlier or not at all. If the six Tuttle plot locations were indeed heavily logged, the stands in these locations were approximately 70 years old by 2004. All other Miller and Tuttle plots are located in areas mapped as selectively cut or unlogged.

Stand summary, species composition, and structure.   Mean plot basal area is similar for the Miller and Tuttle data (43.56 and 42.13 m^2/ha, respectively), but mean plot density is higher for
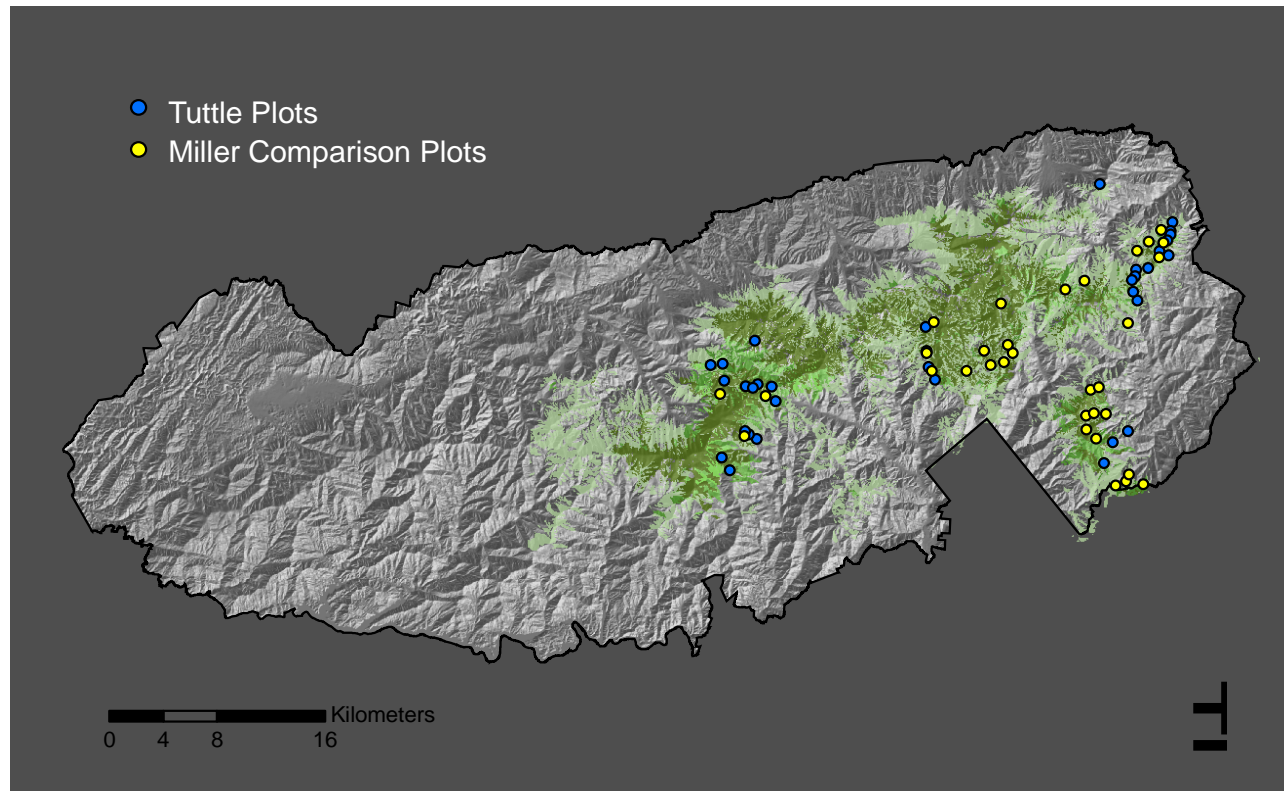
Figure 2. Location of Miller comparison plots (1930s) and Tuttle plots (2004) in the study area of Great Smoky Mountains National Park.

Table 1. Range of topographic and environmental setting for the Miller and Tuttle samples.
*See Results section for explanation.

	Miller	Tuttle
No. plots	32	34
No. plots with history of low to no disturbance*	31	28
Elevation (m)	1240-1707	1203-1706
Slope steepness (%)	18-125	17-72
Slope aspect classes*	1-2, 4-8	1-2, 4-8
TCI	4.02-7.33	3.47-9.52

the Tuttle data (538.6 vs. 409.7 stems/ha, p=0.015, corrected α=0.02) (Table 2). Mean plot species richness is also higher for the Tuttle plots (p=0.0011, corrected α=0.01), while evenness is lower, but this difference is not statistically significant (p=0.0427, corrected α=0.03). Shannon's diversity index is similar for the two data sets.

Total number of species recorded is 20 for the Miller data and 21 for the Tuttle data (Table 2). *Betula alleghaniensis*, *Picea rubens*, and *Fagus grandifolia* are the most widespread species in the Miller data (75, 72, and 68% of plots, respectively) and the dominant species by IV (33, 50, and 38, respectively) (Table 3). For the Tuttle data, *B. alleghaniensis* and *P. rubens* are the most widespread (88 and 82% of plots, respectively) and dominant (46 and 62, respectively) species. Subdominant species in the Miller data include *Abies fraseri*, *Tsuga canadensis*, *Aesculus flava*, and *Acer saccharum*, while *T. canadensis*, *Halesia tetraptera var. monticola*, and *F. grandifolia* are subdominants in the Tuttle data.

Differences in several species' mean basal area and density contribute to these shifts in overstory dominance as well as understory composition (Table 3). Mean density for both *P. rubens* and *B. alleghaniensis* in the Tuttle data is approximately twice the density for the Miller data, while *F. grandifolia* basal area and density in the Tuttle data are less than half those in the Miller data. *Abies fraseri* basal area is reduced by 85% and density by greater than 50% in the Tuttle data. *Tsuga canadensis* density in the Tuttle data is double that of the Miller data, and *H. tetraptera* basal area and density are several times greater in the Tuttle data. *Aesculus flava* basal area is much lower in the Tuttle data. Distribution and abundance of several *Acer* species, including *A. pensylvanicum*, *A. spicatum*, and *A. rubrum*, are much higher in the Tuttle data.

Comparison of Tuttle to Miller overall size-class distributions reveals a 57% increase in stem density in the smallest size class with a 50% reduction in stem density for size class 3 (Figure 3).

Table 2. Summary of stand basal area, density, and diversity for the Miller and Tuttle data.
Tuttle values significantly different from Miller values are noted: * p<0.02, ** p<0.01.

	No. species recorded	Mean plot basal area (m^2/ha)	Mean plot density (stems/ha)	Mean species richness	Mean species evenness	Mean Shannon's Diversity Index
Miller	20	43.56	409.70	4.80	0.74	1.13
Tuttle	21	42.13	538.60*	6.20**	0.66	1.18

Table 3. Mean plot species abundances and frequency of occurrence for the Miller and Tuttle data.

Species	Freq. (% plots)	Basal area (m²/ha) Mean	SD	Density (stems/ha) Mean	SD	Importance Value Mean	SD	Freq. (% plots)	Basal area (m²/ha) Mean	SD	Density (stems/ha) Mean	SD	Importance Value Mean	SD
		MILLER							TUTTLE					
Abies fraseri (ABFR)	28.13	2.40	4.95	54.66	110.60	14.19	26.69	17.65	0.35	1.60	23.53	101.40	3.59	14.27
Acer pensylvanicum (ACPE)	9.38	0.03	0.08	1.13	3.55	0.58	2.22	55.88	0.44	0.59	20.22	27.01	5.66	7.11
Acer rubrum (ACRU)	3.13	0.16	0.92	1.16	6.54	0.85	4.80	26.47	1.42	3.59	13.24	31.82	6.07	14.59
Acer saccharum (ACSA)	43.75	2.75	3.93	12.91	18.58	11.39	15.89	38.24	1.52	3.40	18.01	36.57	8.17	15.45
Acer spicatum (ACSP)	3.13	0.01	0.05	0.38	2.12	0.37	2.07	23.53	0.22	0.66	9.56	22.42	2.18	5.16
Aesculus flava (AEFL)	28.13	3.65	9.10	5.31	11.98	12.31	28.53	35.30	1.29	2.51	9.56	16.87	5.78	10.31
Amelanchier laevis (AMLA)	21.88	0.17	0.39	14.12	37.58	1.79	4.10	17.65	0.22	0.68	2.94	7.58	1.10	2.99
Betula lenta (BELE)	15.63	0.67	2.10	8.03	22.61	3.46	9.46	17.65	0.55	1.83	8.09	26.63	3.28	10.90
Betula alleghaniensis (BEAL)	75.0	7.14	8.55	54.87	52.64	33.08	31.81	88.24	10.55	9.71	109.90	117.40	46.11	38.43
Carya sp. (CASP)	0							5.88	0.22	0.94	1.47	5.97	0.81	3.34
Cornus alternifolia (COAL)	0							2.94	0.02	0.14	0.74	4.29	0.24	1.39
Castanea dentata (CADE)	3.13	0.01	0.05	0.38	2.12	0.19	1.08	0						
Fagus grandifolia (FAGR)	68.75	4.14	6.0	95.78	125.60	38.25	46.39	41.18	2.0	4.05	46.69	108.60	13.27	25.31
Fraxinus americana (FRAM)	6.25	0.16	0.67	1.13	4.68	0.60	2.35	0						
Halesia tetraptera var. monticola (HATR)	28.13	0.54	1.18	8.03	14.83	3.76	7.63	47.06	3.06	5.16	34.93	49.79	14.92	21.20
Magnolia acuminata (MAAC)	3.13	0.05	0.31	0.38	2.12	0.22	1.24	0						
Magnolia fraseri (MAFR)	0							8.82	0.02	0.07	1.47	5.12	0.42	1.42
P. rubens (PIRU)	71.88	14.80	23.43	106.60	137.20	50.06	50.00	82.35	13.33	13.65	181.60	173.40	62.36	50.93
Prunus pensylvanica (PRPE)	9.38	0.28	1.05	12.72	47.08	4.15	14.09	17.65	0.21	0.67	6.62	24.08	1.44	4.41
Prunus serotina (PRSE)	0							5.88	0.51	2.10	1.84	8.78	1.80	7.35
Quercus rubra (QURU)	12.5	1.09	4.18	7.28	28.96	6.55	22.80	8.82	1.24	5.26	4.78	21.76	3.08	12.31
Sorbus americana (SOAM)	3.13	0.01	0.05	0.38	2.12	0.13	0.71	5.88	0.03	0.11	1.47	5.97	0.24	0.99
Tilia americana var. heterophylla (TIHE)	15.63	1.02	2.98	4.56	15.80	4.35	12.45	8.82	0.38	1.51	2.21	7.83	1.19	4.57
Tsuga canadensis (TSCA)	31.25	4.49	8.44	19.94	34.59	14.88	24.73	58.82	4.46	11.14	38.60	52.44	17.77	31.10
Unknown	0							8.82	0.13	0.63	1.10	3.60	0.52	2.10
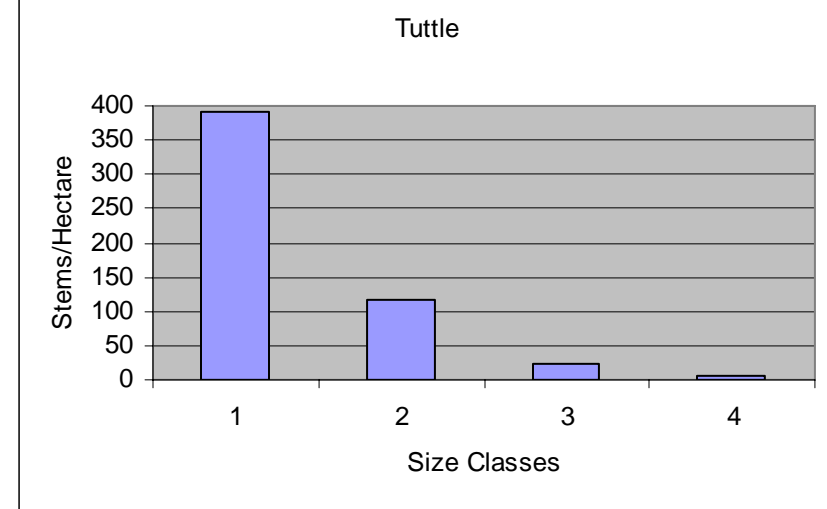
Figure 3. Size-class distributions for the Miller and Tuttle data based on total plot density. Species abbreviations are as in Table 3 and consist of the first two letters of the genus followed by the first two letters of the species (e.g., PIRU = *Picea rubens*). Size classes are as in text: 1 = 10.1-30.3 cm; 2 = 30.4-60.8 cm; 3 = 60.9-90.3 cm; 4 = >90.3 cm.

Species size-class distributions elaborate these differences (Figures 4, 5): In size class 1, much higher stem densities for *P. rubens*, *B. alleghaniensis*, *T. canadensis*, *H. tetraptera*, and all *Acer* species overwhelm the 50% lower stem densities of *A. fraseri* and *F. grandifolia*, but similar decreases in class 2 offset higher stem densities for *P. rubens*, *B. alleghaniensis*, and *H. tetraptera* with no overall difference in this size class. For size class 3, stem density "losses" in *P. rubens*, *T. canadensis*, *A. saccharum*, *A. flava*, and *Betula lenta* are greater than "gains" for *H. tetraptera* and *A. rubrum*. For size class 4, a slightly greater stem density overall can be attributed to higher stem densities for *T. canadensis*, *P. rubens,* and *F. grandifolia* that more than offset the lower stem densities of *A. flava* and *A. saccharum*. *Betula alleghaniensis* stem densities for size classes 3 and 4 are similar in the two data sets.

Stand summary and species composition by elevation. Clear trends in mean plot basal area from low to high elevation are not immediately apparent in either data set (Figure 6a), and small sample sizes in elevation zones 1 and 2 prohibit reliable interpretation of values for those zones. For zones 3-5, Miller basal area is highest for zone 5. Tuttle basal area is similar across zones 3-5 without an increase comparable to the Miller data for zone 5. Miller density exhibits a pattern similar to basal area for zones 3-5 (Figure 6b). In contrast, the Tuttle data exhibit a general trend of increasing density with elevation with a slight decrease for zone 5. Principal differences between the two data sets include higher Miller basal area for zone 5 and higher Tuttle density for zones 3 and 4.
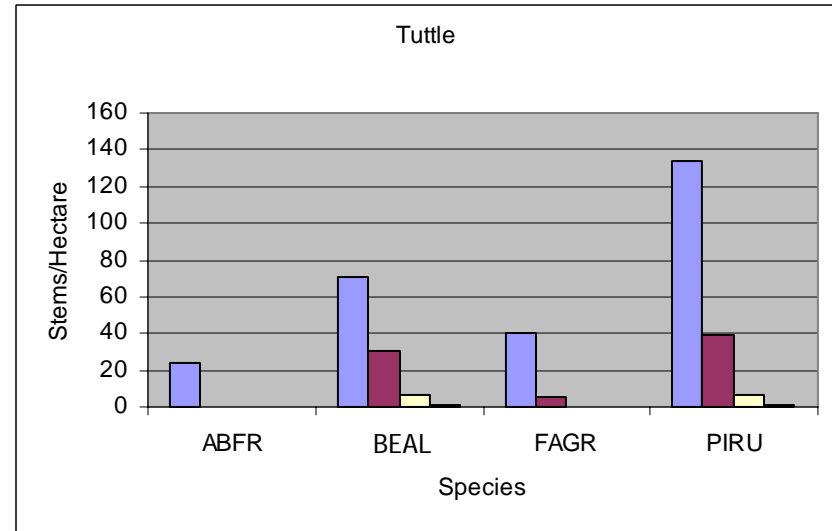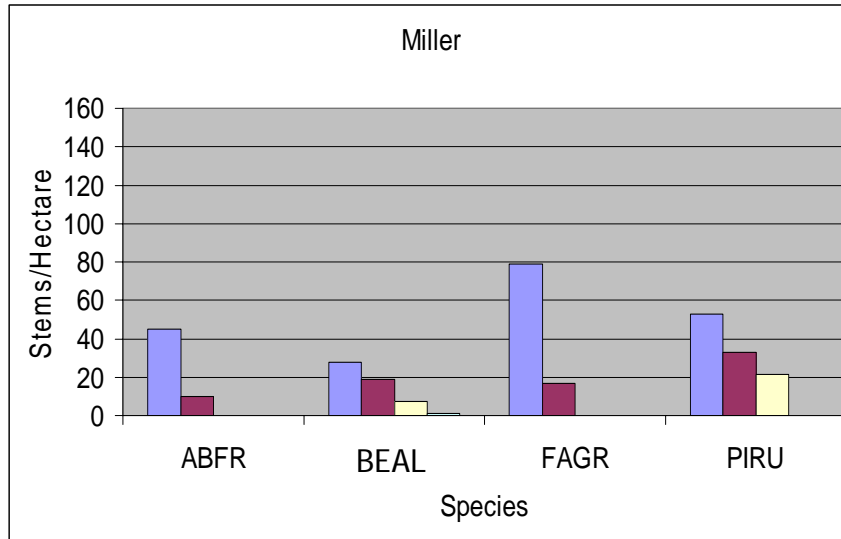
Figure 4. Size-class distributions for species with the highest densities in the Miller or Tuttle data. Species abbreviations are as in Table 3. Size classes are as in text: blue = 1 (10.1-30.3 cm); maroon = 2 (30.4-60.8 cm); yellow = 3 (60.9-90.3 cm); pale aqua = 4 (>90.3 cm).
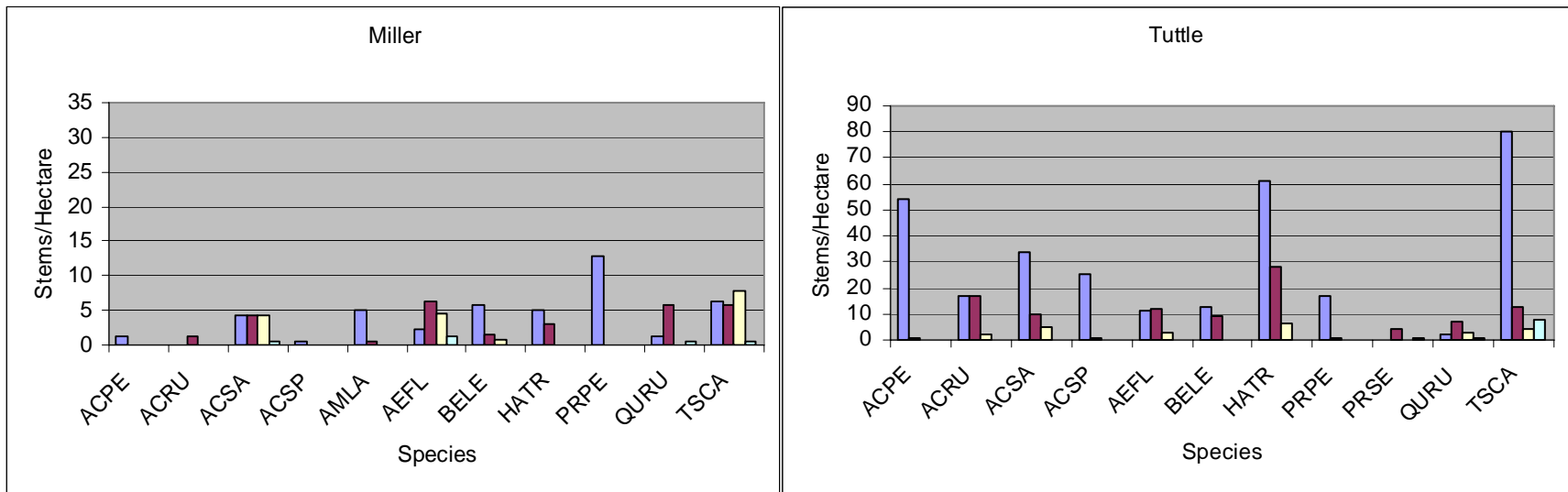
Figure 5. Size-class distributions for other important species in the Miller and Tuttle data. Species abbreviations are as in Table 3. Size classes are as in text: blue = 1 (10.1-30.3 cm); maroon = 2 (30.4-60.8 cm); yellow = 3 (60.9-90.3 cm); pale aqua = 4 (>90.3 cm).
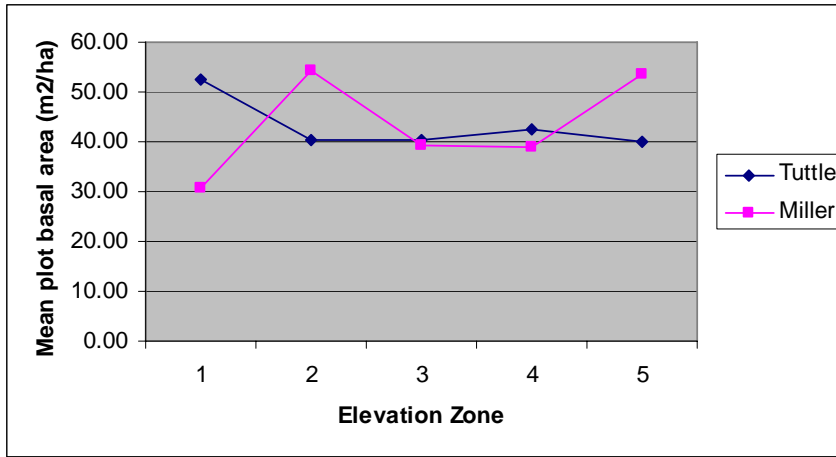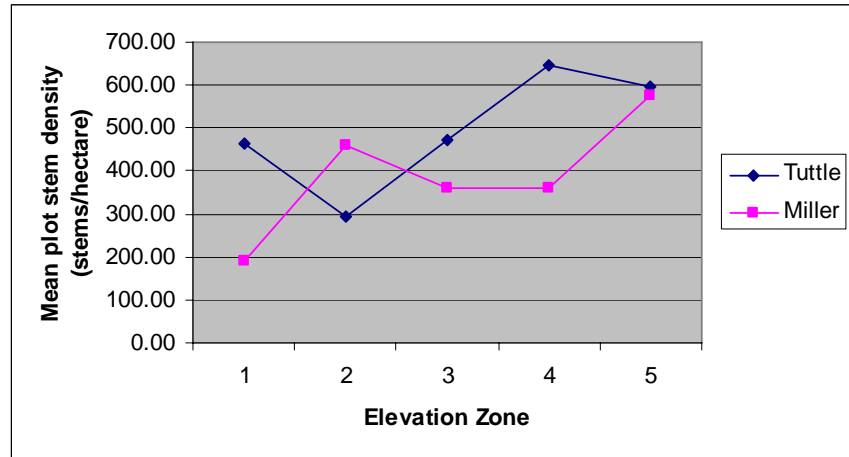
(a)   (b)

Figure 6. Mean plot basal area (m^2/ha) **(a)** and density (stems/ha) **(b)** by elevation zone for the Miller and Tuttle data. Elevation zones are as in text: 1 = 1200-1300 m; 2 = 1300-1400 m; 3 = 1400-1500 m; 4 = 1500-1600 m; 5 = 1600-1710 m.

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Inspection of dominant species composition by elevation elaborates these and other differences. For the Miller data, *B. alleghaniensis*, *A. flava*, *T. canadensis*, and *F. grandifolia* codominate between 1200 and 1400 m (Figures 7-9). *Tsuga canadensis* and *A. flava* generally decrease in importance with increasing elevation, although *T. canadensis* remains an important subdominant through 1500 m. *Betula alleghaniensis* exhibits a somewhat U-shaped importance curve with elevation, but remains important between 1400 and 1600 m, while *F. grandifolia* increases in importance, and *P. rubens* emerges as its codominant. *Fagus grandifolia* is important primarily because of high densities, and *P. rubens* clearly dominates by basal area. *Abies fraseri* is first present in plots above 1400 m. By 1600-1700 m, *P. rubens* is the most important species with *A. fraseri* and *B. alleghaniensis* secondarily important. *Fagus grandifolia* drops to minimal importance in this zone.

For the Tuttle data, *T. canadensis* dominates between 1200 and 1300 m with subdominants of *H. tetraptera*, *B. alleghaniensis*, and *A. saccharum* (Figures 7-9). *Tsuga canadensis* continues to dominate between 1300 and 1400 m with a shift in subdominance to *H. tetraptera* and *P. rubens*. *Tsuga canadensis*, *H. tetraptera*, and *A. saccharum* all generally decrease in importance with increasing elevation and are of minimal or no importance by 1500 m. *Picea rubens* and *B. alleghaniensis* both generally increase in importance with increasing elevation and codominate between 1400 and 1500 m. Between 1500 and 1700 m, *P. rubens* and *B. alleghaniensis* are the only important species, and *P. rubens* dominates. *Abies fraseri* is only minimally present above 1500 m and becomes slightly important by 1600-1700 m because of high density.

Comparison of these species trends with elevation reveals the primary differences in dominance between the two data sets (Figures 7-9): *Abies fraseri* and *F. grandifolia* basal area and density are much lower in the Tuttle data across all elevations where they occur (zones
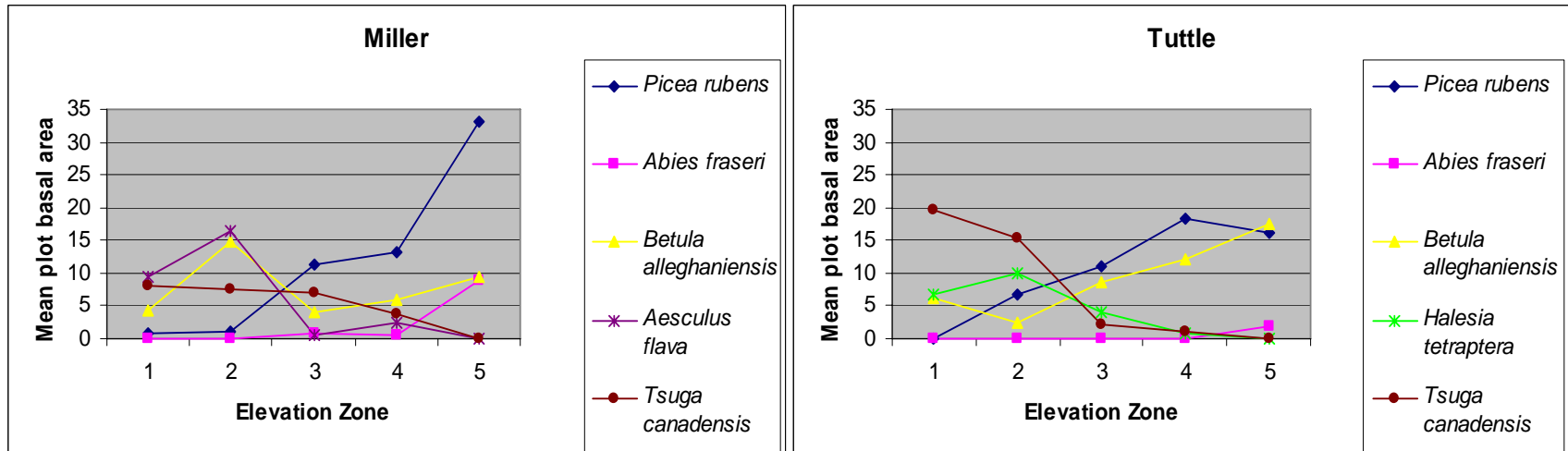
Figure 7. Mean species basal area (m^2/ha) by elevation zone for the Miller and Tuttle data. Elevation zones are as in text: 1 = 1200-1300 m; 2 = 1300-1400 m; 3 = 1400-1500 m; 4 = 1500-1600 m; 5 = 1600-1710 m.
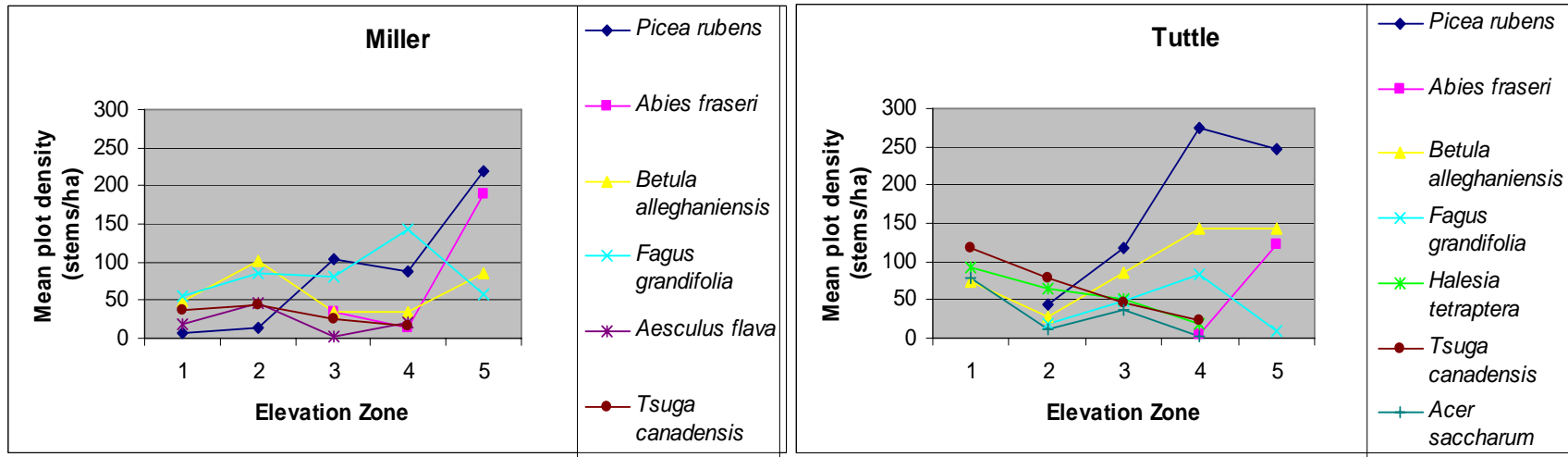
Figure 8. Mean species density (stems/ha) by elevation zone for the Miller and Tuttle data. Elevation zones are as in text: 1 = 1200-1300 m; 2 = 1300-1400 m; 3 = 1400-1500 m; 4 = 1500-1600 m; 5 = 1600-1710 m.
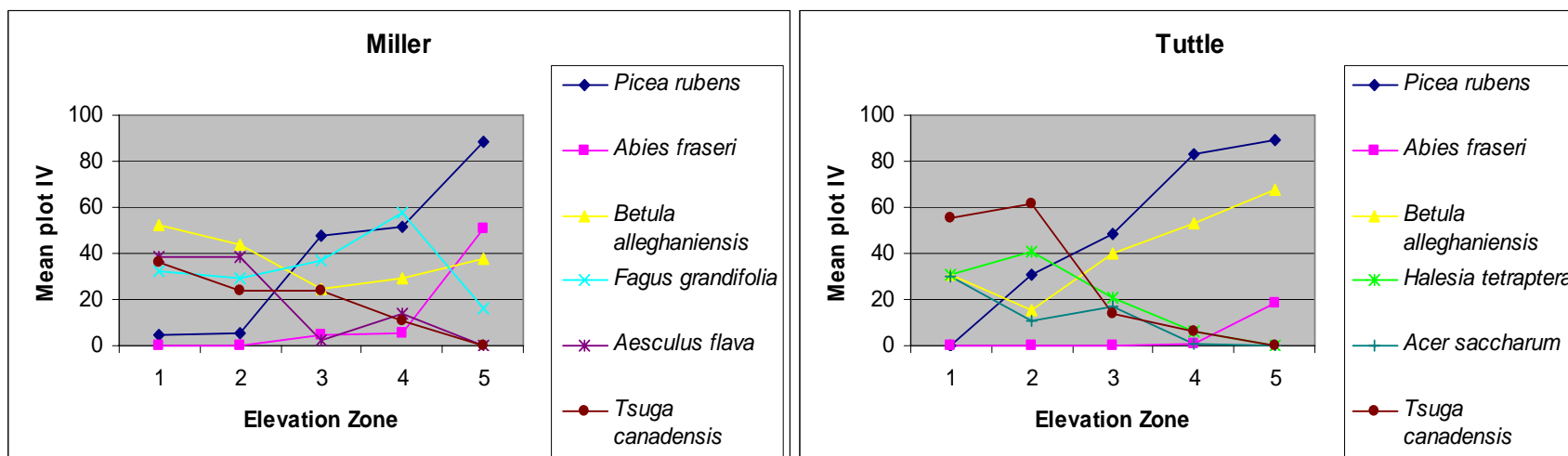
Figure 9. Mean species importance value (IV) by elevation zone for the Miller and Tuttle data. Elevation zones are as in text: 1 = 1200-1300 m; 2 = 1300-1400 m; 3 = 1400-1500 m; 4 = 1500-1600 m; 5 = 1600-1710 m.

3-5 for *A. fraseri* and 1-5 for *F. grandifolia*). *Picea rubens* density is higher in the Tuttle data for elevation zones 2-5, most dramatically for zone 4. Basal area, however, is higher only in zones 2 and 4, approximately the same in zone 3, and lower by more than 50% in zone 5. *Betula alleghaniensis* basal area and density are higher in the Tuttle data for all but elevation zone 2, with the most pronounced differences in zones 3-5. Both measures are much lower in elevation zone 2. There is clear dominance by *T. canadensis* in zones 1 and 2 for the Tuttle data and more mixed dominance of several species for the Miller data. Other notable differences in the Tuttle data include higher density of the disturbance-related *Sorbus americana* in zone 5 and much higher basal area and density of several *Acer* species across all zones, including *A. pensylvanicum*, *A. spicatum*, and *A. rubrum*.

   The increases in overall mean plot density in the Tuttle data for elevation zones 3 and 4 (Figure 6b) are driven largely by higher densities for *B. alleghaniensis* and *P. rubens*. Lower basal area for *P. rubens* and *A. fraseri* in zone 5 drives the lower overall mean plot basal area for the Tuttle data (Figure 6a). However, again, because of the small sample sizes in zones 1 and 2, differences in dominant species for these zones, as well as the overall differences in mean plot basal area and density (Figure 6a,b), may reflect inadequate sampling of the diverse community types at these elevations rather than a temporal shift in dominance.

   Community types.   Cluster analyses of plots by basal area using Ward's method and relative Euclidean distance produced solutions with minimal chaining for the Miller, Tuttle, and combined Miller-Tuttle data sets. An eight-cluster solution for the combination data set delineated communities broadly dominated or structured by conifers (*P. rubens* or *T. canadensis*), northern hardwoods (*B. alleghaniensis; Quercus rubra; F. grandifolia-A. saccharum; A. flava-F. grandifolia-B. alleghaniensis;* or *A. saccharum-H. tetraptera*), or

northern hardwoods-conifer (*F. grandifolia-P. rubens*). Both the *P. rubens* and *T. canadensis* types are well represented in each data set. The *A. saccharum-H. tetraptera* type consists of Tuttle plots only. The remaining northern hardwood types, excluding *Q. rubra*, consist primarily of either Miller or Tuttle plots, most notably the *B. alleghaniensis* type, which includes 23.5% of the Tuttle plots but only 6.3% of the Miller plots. A six-cluster solution for each of the separate data sets yielded similar types with four common to both Miller and Tuttle, including *P. rubens*, *B. alleghaniensis*, *F. grandifolia*, and *T. canadensis*. The Miller data include an *A. flava* type, and the Tuttle data include an *A. saccharum* type and an *A. rubrum-Q. rubra* type.

  Community gradients. Nonmetric multidimensional scaling (NMS) of plot composition by basal area for the combined data sets yielded a statistically significant (p=0.0196) three-dimensional solution with a cumulative r^2 of 0.829. The data sets encompass a similar range of compositional variation with much overlap of Miller and Tuttle plots (Figure 10). Elevation as the dominant compositional gradient is best represented by axis 1, which explains most of the variance in plot dissimilarity ($r^2 = 0.473$) and is indeed positively correlated with plot elevation ($r = 0.542$) (Figure 10). Aspect class and slope are most strongly correlated with axis 3 ($r = 0.404$ and $r = 0.221$, respectively), and TCI is the weakest of the topographic variable-axis correlations. Species-axis correlations indicate which species most structure the compositional gradients represented by the axes (Table 4). For example, *P. rubens* and *A. fraseri* are positively correlated with axis 1, while lower elevation species such as *A. saccharum* and *A. flava* are negatively correlated. *Tsuga canadensis* and *H. tetraptera* most contribute to structure along axis 2. Wide-ranging species such as *B. alleghaniensis* and *F. grandifolia* are correlated with all three axes. Plotting the combined Ward's cluster types on the ordination diagram further illustrates how these dominant species, as indicators of community (and likely
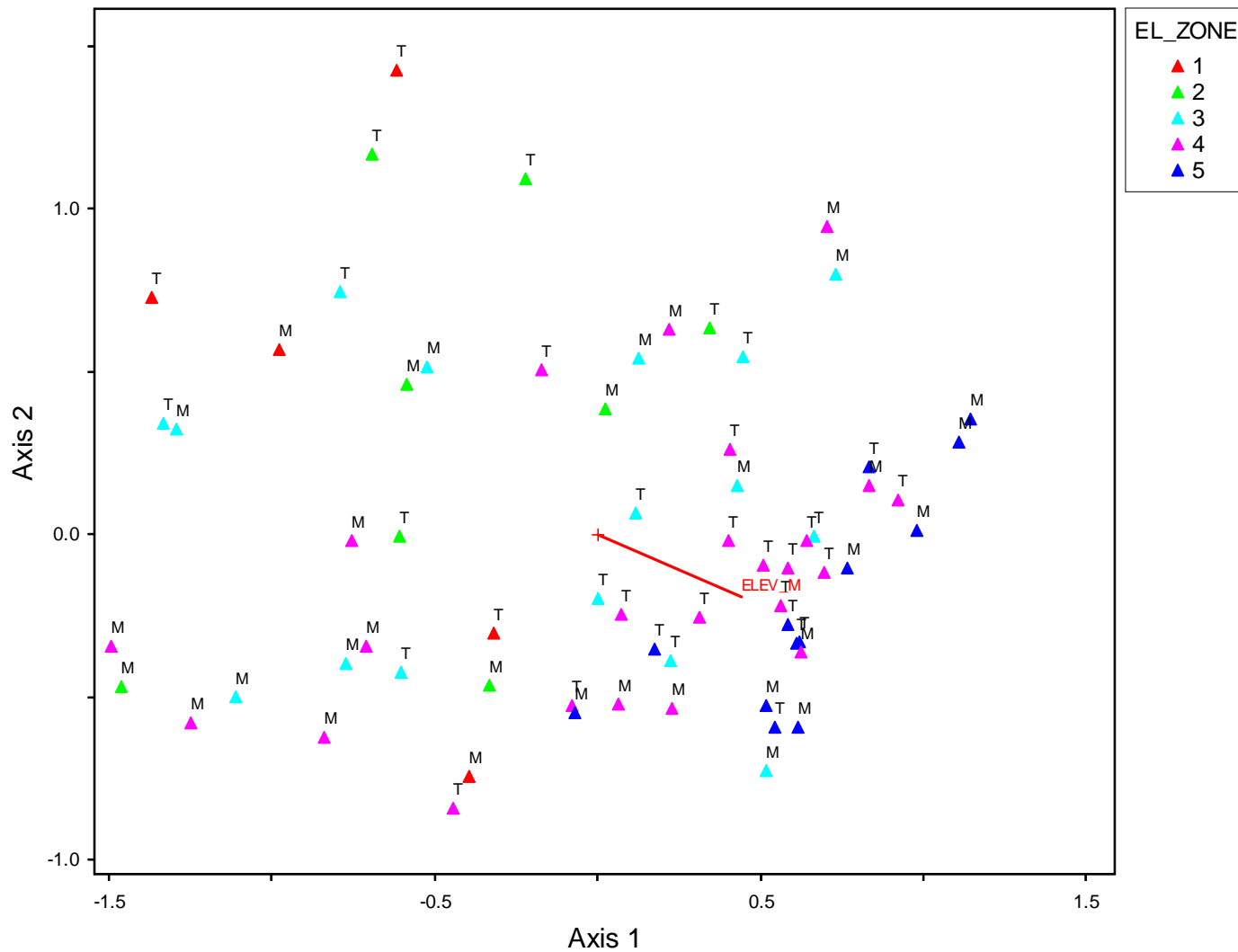
Figure 10. Nonmetric multidimensional scaling (NMS) of the Miller (M) and Tuttle (T) plots combined as one data set. EL_ZONE refers to elevation zones as in text: 1 = 1200-1300 m; 2 = 1300-1400 m; 3 = 1400-1500 m; 4 = 1500-1600 m; 5 = 1600-1700 m. Cumulative r^2 = 0.829, final stress 13.77543 (significant by Monte Carlo randomization test, p = 0.0196), final instability 0.00001,. Elevation (m) (vector ELEV_M) is correlated with axes 1 (r = 0.542) and 2 (r = -0.356).

Table 4. Pearson correlations of species basal area with ordination axes for nonmetric multidimensional scaling (NMS) of the combined Miller and Tuttle data. Species abbreviations are as in Table 3.

	Axis 1		Axis 2		Axis 3	
	r	r^2	r	r^2	r	r^2
ABFR	0.427	0.182	-0.019	0	-0.094	0.009
ACPE	0.039	0.001	-0.071	0.005	0.062	0.004
ACRU	-0.116	0.013	0.122	0.015	-0.343	0.118
ACSA	-0.714	0.509	0.007	0	-0.024	0.001
ACSP	0.048	0.002	0.004	0	-0.024	0.001
AEFL	-0.423	0.179	-0.164	0.027	0.298	0.089
AMLA	-0.002	0	-0.063	0.004	-0.322	0.104
BELE	-0.057	0.003	0.044	0.002	0.142	0.02
BEAL	0.396	0.157	-0.333	0.111	0.661	0.437
CADE	-0.093	0.009	0.125	0.016	-0.079	0.006
CARSP	-0.328	0.108	0.196	0.038	0.025	0.001
COAL	-0.078	0.006	-0.203	0.041	0.04	0.002
FAGR	-0.47	0.221	-0.408	0.166	-0.461	0.213
FRAM	-0.155	0.024	-0.065	0.004	0.121	0.015
HATR	-0.261	0.068	0.563	0.317	0.098	0.01
MAAC	-0.258	0.066	-0.113	0.013	0.009	0
MAFR	0.023	0.001	0.209	0.044	-0.096	0.009
PIRU	0.683	0.467	0.239	0.057	-0.164	0.027
PRPE	0.164	0.027	-0.083	0.007	0.249	0.062
PRSE	-0.256	0.066	0.195	0.038	-0.128	0.016
QURU	-0.242	0.059	0.157	0.025	-0.095	0.009
SOAM	0.113	0.013	-0.195	0.038	-0.026	0.001
TIHE	-0.364	0.133	-0.021	0	0.132	0.017
TSCA	-0.069	0.005	0.728	0.529	0.202	0.041
UNK	0.072	0.005	0.148	0.022	-0.053	0.003

site) types, structure the combined ordination space (Figure 11). In general, the *P. rubens* and *B. alleghaniensis* types are clustered at the high-elevation end of axis 1, and the *T. canadensis* type is separated from the *F. grandifolia*-related clusters by axis 2. The three *F. grandifolia* types in turn are distinguished from each other by axis 3 (not shown).

  NMS of the Miller and Tuttle data sets separately again yielded statistically significant three-dimensional solutions with cumulative r^2 of .798 and .887, respectively (Figures 12, 13). Elevation is again the dominant gradient for both data sets. However, this gradient is much more pronounced in the Tuttle data with a strong correlation of elevation with the primary explanatory axis (r = 0.764, axis 3), whereas for the Miller data, elevation is most correlated with the weaker explanatory axes (r = 0.439, axis 2 and r = 0.313, axis 3). Slope and aspect class are instead the most important topographic variable correlations for the primary Miller axis, and TCI is relatively uncorrelated with the axes. For the Tuttle data, TCI and aspect class are correlated with axis 2 and slope with axis 3. Species-axis correlations for the separate ordinations similarly reveal how the dominant species structure ordination space. For the Miller data, *A. fraseri*, *P. rubens*, *A. saccharum*, and *F. grandifolia* most strongly structure axis 2, while *T. canadensis* and *F. grandifolia* are correlated with axis 1 and *A. flava* with axis 3 (Table 5). For the Tuttle data, the strongest correlations are concentrated on axis 3, including *P. rubens*, *H. tetraptera*, *A. saccharum*, and *T. canadensis*. *Fagus grandifolia* is correlated with axis 2, *B. alleghaniensis* with both axes 2 and 3, and *P. rubens* and *T. canadensis* with axis 1 (Table 6). Again the dominance of these species is illustrated by plotting the separate Ward's cluster types on the ordination diagrams (Figures 12, 13), with cluster types more clearly defined here than on the combined ordination.
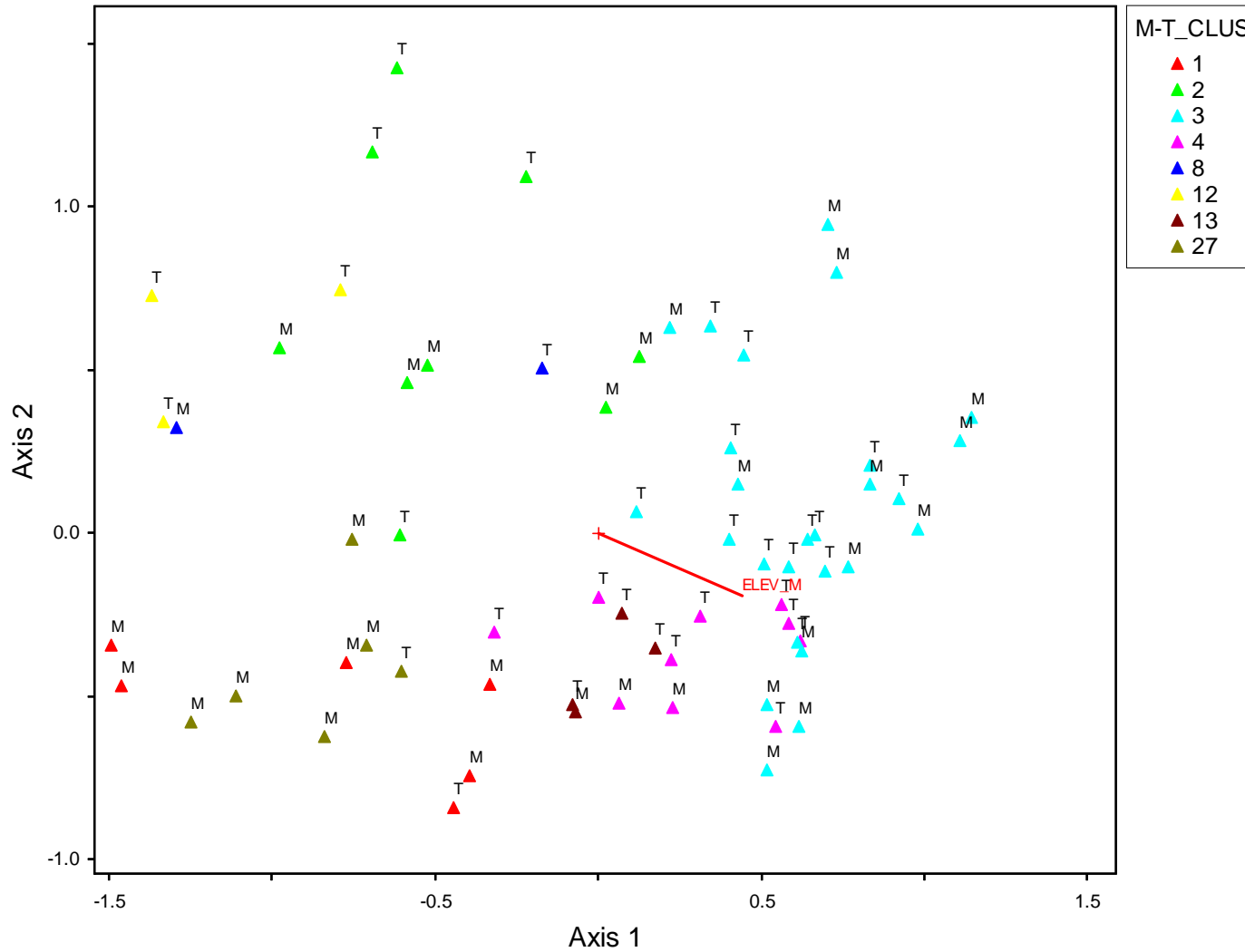
Figure 11. NMS of the combined Miller (M) and Tuttle (T) plots, with cluster types from the ***combined*** Miller-Tuttle cluster analysis:
1 = *Aesculus flava-Fagus grandifolia-Betula alleghaniensis*, 2 = *Tsuga canadensis*, 3 = *Picea rubens*, 4 = *B. alleghaniensis*, 8 = *Quercus rubra*, 12 = *Acer saccharum-Halesia tetraptera*, 13 = *F. grandifolia-P. rubens*, 27 = *F. grandifolia-A. saccharum.* The vector ELEV_M shows correlation of elevation (m) with axes 1 and 2.
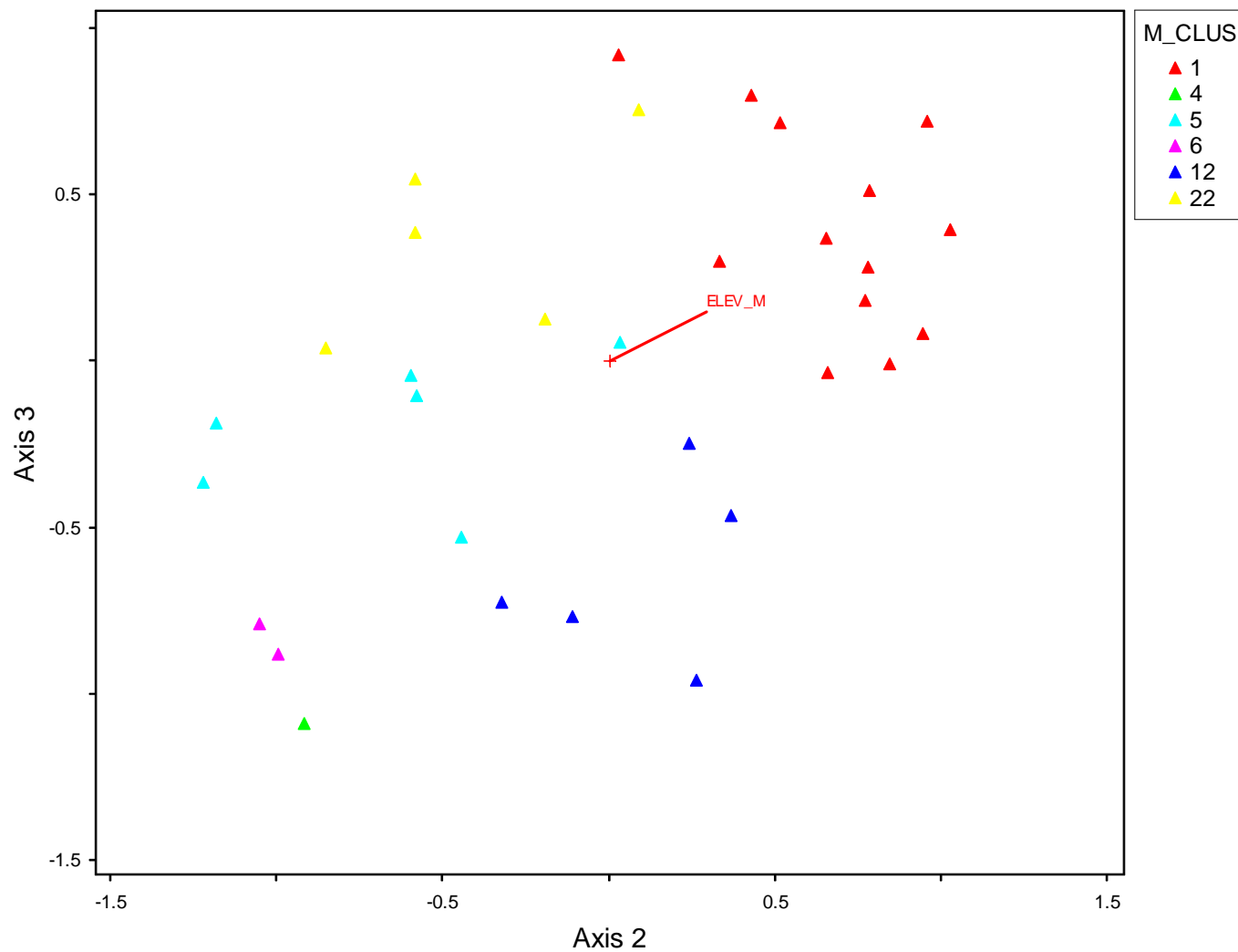
Figure 12. NMS of the Miller data, with cluster types: 1 = *Picea rubens*, 4 = *Quercus rubra*, 5 = *Fagus grandifolia*, 6 = *Aesculus flava*, 12 = *Betula alleghaniensis*, 22 = *Tsuga canadensis*. Cumulative $r^2 = 0.798$, final stress 12.41349 (significant by Monte Carlo test, p = 0.0196), final instability 0.00013. Elevation (m) (vector ELEV_M) is correlated with axes 2 (r = 0.439) and 3 (r = 0.313).
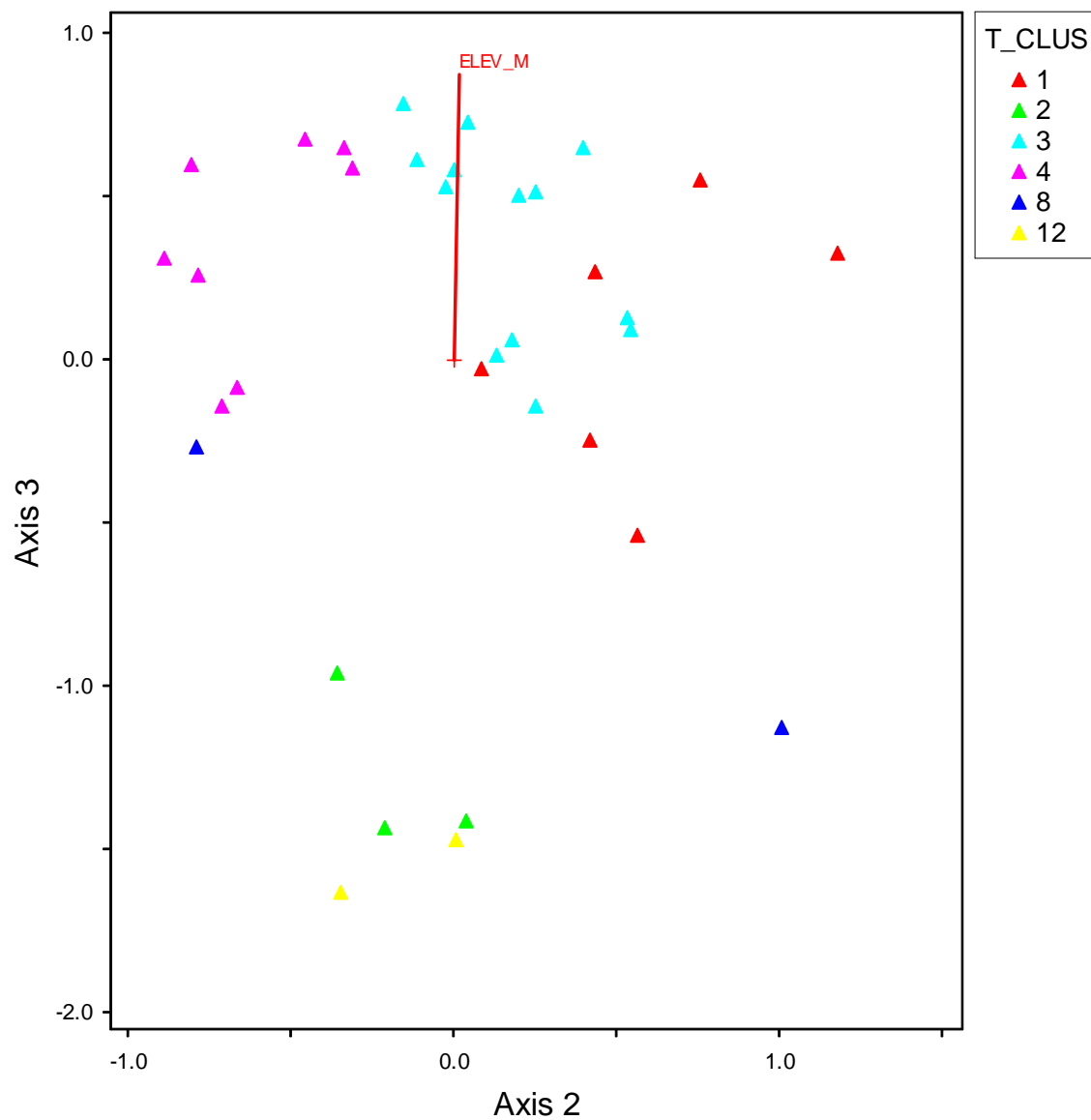
Figure 13. NMS of the Tuttle data, with cluster types: 1 = *Fagus grandifolia*, 2 = *Tsuga canadensis*, 3 = *Picea rubens*, 4 = *Betula alleghaniensis*, 8 = *Quercus rubra*, 12 = *Acer saccharum*. Cumulative r^2 = 0.887, final stress 11.06935 (significant by Monte Carlo test, p = 0.0196), final instability 0.00001. Elevation (m) (vector ELEV_M) is correlated with axis 3 (r = 0.764).

Table 5. Pearson correlations of species basal area with ordination axes for the Miller NMS. Species abbreviations are as in Table 3.

	Axis 1		Axis 2		Axis 3	
	r	r^2	r	r^2	r	r^2
ABFR	-0.17	0.029	-0.278	0.078	0.184	0.034
ACPE	-0.231	0.054	0.087	0.008	0.053	0.003
ACRU	0.013	0	0.445	0.198	-0.122	0.015
ACSA	-0.275	0.076	-0.029	0.001	-0.598	0.357
ACSP	-0.003	0	0.109	0.012	0.025	0.001
AEFL	-0.296	0.088	-0.065	0.004	-0.385	0.148
AMLA	-0.058	0.003	0.37	0.137	0.106	0.011
BELE	-0.355	0.126	-0.301	0.09	0.046	0.002
BEAL	-0.166	0.028	-0.632	0.399	0.573	0.329
CASP	-0.113	0.013	-0.104	0.011	-0.537	0.288
COAL	-0.387	0.15	0.028	0.001	-0.006	0
FAGR	-0.4	0.16	0.564	0.318	0.128	0.016
HATR	0.445	0.198	-0.043	0.002	-0.695	0.484
MAFR	0.261	0.068	0.178	0.032	-0.142	0.02
PIRU	0.497	0.247	0.253	0.064	0.61	0.372
PRPE	-0.102	0.01	-0.301	0.091	0.282	0.079
PRSE	-0.143	0.02	0.273	0.075	-0.448	0.201
QURU	0.164	0.027	-0.275	0.076	-0.154	0.024
SOAM	-0.167	0.028	0.037	0.001	0.201	0.041
TIHE	0.202	0.041	-0.145	0.021	-0.546	0.298
TSCA	0.538	0.289	-0.125	0.016	-0.546	0.298
UNK	0.233	0.054	0.1	0.01	-0.015	0

Table 6. Pearson correlations of species basal area with ordination axes for the Tuttle NMS. Species abbreviations are as in Table 3.

	Axis 1		Axis 2		Axis 3	
	r	r^2	r	r^2	r	r^2
ABFR	0.222	0.049	0.61	0.372	0.324	0.105
ACPE	0.144	0.021	0.063	0.004	-0.114	0.013
ACRU	-0.239	0.057	-0.239	0.057	-0.356	0.126
ACSA	-0.185	0.034	-0.687	0.472	-0.413	0.17
ACSP	0.033	0.001	0.094	0.009	-0.151	0.023
AEFL	0.365	0.133	-0.35	0.122	-0.515	0.265
AMLA	-0.214	0.046	-0.052	0.003	-0.202	0.041
BELE	-0.036	0.001	-0.144	0.021	0.333	0.111
BEAL	0.323	0.104	0.318	0.101	-0.237	0.056
CADE	0.029	0.001	-0.152	0.023	0.127	0.016
FAGR	-0.518	0.268	-0.659	0.435	-0.36	0.13
FRAM	0.126	0.016	-0.135	0.018	-0.388	0.151
HATR	-0.082	0.007	-0.34	0.115	-0.026	0.001
MAAC	0.116	0.013	-0.259	0.067	-0.288	0.083
PIRU	0.534	0.285	0.603	0.364	0.449	0.202
PRPE	0.183	0.034	0.064	0.004	0.103	0.011
QURU	-0.363	0.132	-0.344	0.119	-0.342	0.117
SOAM	-0.08	0.006	0.17	0.029	-0.011	0
TIHE	-0.123	0.015	-0.182	0.033	-0.437	0.191
TSCA	0.536	0.288	-0.005	0	0.48	0.23

The separate ordinations highlight differences in the two data sets noted previously, such as the decrease in importance of *A. fraseri* and *A. flava* and the increase in importance of *B. alleghaniensis* and *H. tetraptera* in the Tuttle data. However, *F. grandifolia* remains an important indicator species for community type even though its dominance is much lower. The communities are organized differently along the dominant gradient (elevation) as well, most prominently the *B. alleghaniensis* community type's closer association in ordination space with the *P. rubens* type for the Tuttle data.

A return to the combined ordination diagram with the separate Ward's cluster types plotted further illustrates differences in community structure between the Miller and Tuttle data (Figure 14): The Tuttle *B. alleghaniensis* type is shifted higher along the elevation-dominated axis than the Miller *B. alleghaniensis* type and overlaps the Miller *P. rubens* plots in which *A. fraseri* was prominent. While the Tuttle *P. rubens* type overlaps the same type for Miller, the cluster is more compact for the Tuttle data. Finally, the *T. canadensis* type for the Tuttle data is notably separate in ordination space from the analogous Miller type.

Species-topography relationships.   Canonical correspondence analysis (CCA) of the separate data sets and topographic variables allowed more rigorous comparison of species- and community-topography relationships in the two data sets. Both ordinations are significant with similar cumulative variance in species scores explained (~23%) (Table 7). Similar to the NMS results, the Tuttle data exhibit a stronger relationship with the primary axis than the Miller data. This difference is reflected in the distribution of topographic variable-axis correlations for the two data sets: While both ordinations are structured similarly, with elevation, slope, and aspect class strongly correlated with axes 1, 2, and 3, respectively, elevation is less strongly correlated and slope and aspect more highly correlated with their respective axes for the Miller data (Table
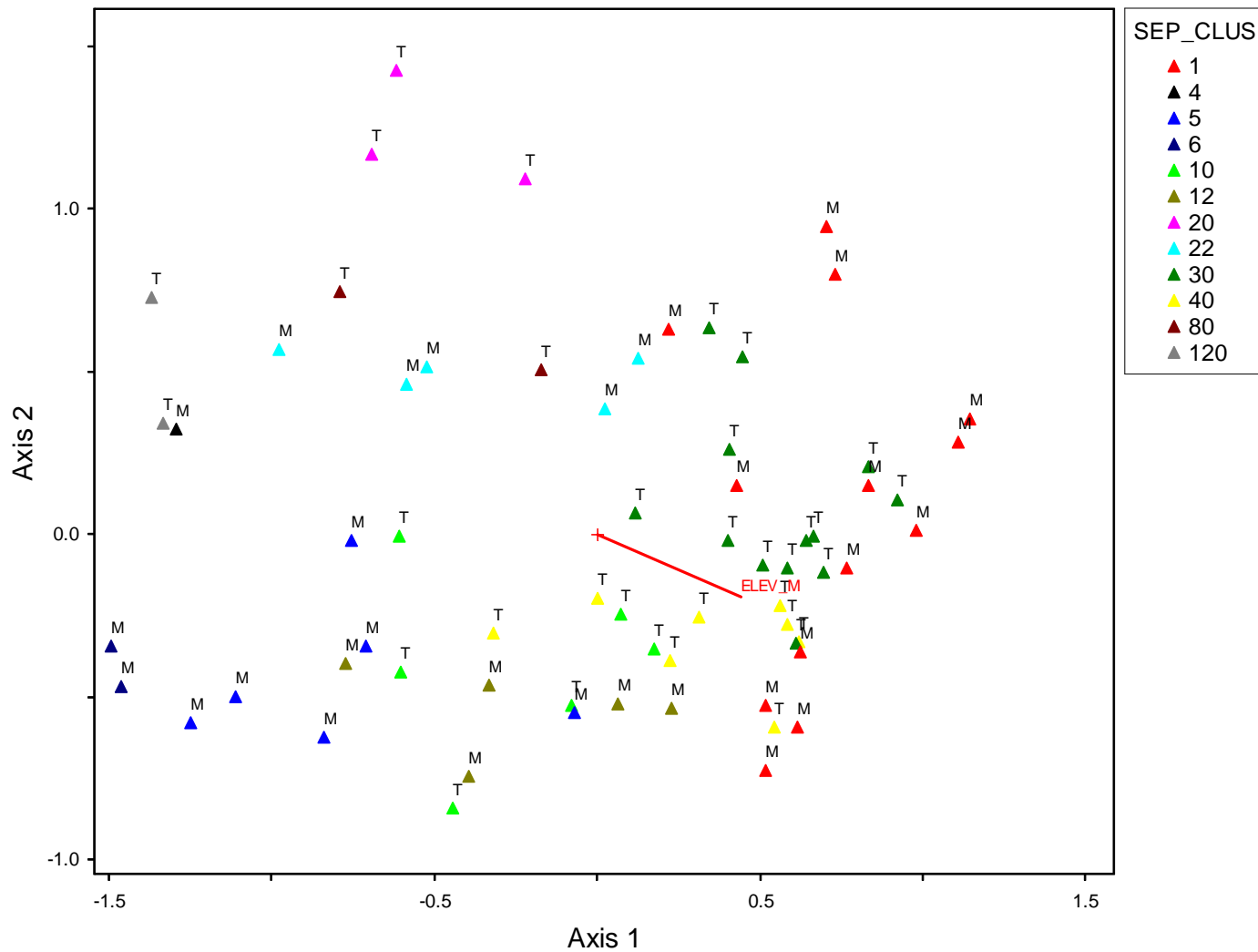
Figure 14. NMS of the combined Miller and Tuttle plots, with cluster types from the ***separate*** Miller and Tuttle cluster analyses: 1 = Miller *Picea rubens*, 4 = Miller *Quercus rubra*, 5 = Miller *Fagus grandifolia*, 6 = Miller *Aesculus flava*, 10 = Tuttle *F. grandifolia*, 12 = Miller *Betula alleghaniensis*, 20 = Tuttle *Tsuga canadensis*, 22 = Miller *T. canadensis*, 30 = Tuttle *P. rubens*, 40 = Tuttle *B. alleghaniensis*, 80 = Tuttle *Acer rubrum-Q. rubra*, 120 = Tuttle *Acer saccharum*. The vector ELEV_M shows correlation of elevation (m) with axes 1 and 2.

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Table 7. Canonical correspondence analysis (CCA) results for the Miller and Tuttle data. Eigenvalues and species-environment correlations for axis 1 are significant by Monte Carlo randomization test (* p=0.0.2, ** p=0.03, *** p=0.01). Total inertia in the species data was 2.9988 for Miller and 3.1651 for Tuttle.

	Miller			Tuttle		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Eigenvalue	0.37*	0.188	0.14	0.52***	0.13	0.09
Variance in species data explained (%)	12.40	6.20	4.60	16.40	4.10	2.90
Cumulative variance explained (%)	12.40	18.60	23.20	16.40	20.50	23.40
Pearson correlations, species-environment	0.77**	0.68	0.61	0.91***	0.59	0.58
Topographic variable correlations						
Elevation (m)	0.89	-0.19	0.31	-0.91	0.22	-0.35
Aspect class	-0.02	0.57	0.82	-0.001	0.54	0.75
Slope steepness (%)	0.19	0.93	-0.24	0.21	0.77	-0.45
TCI	-0.12	0.05	0.21	-0.02	-0.30	0.32

7). TCI is the least important topographic variable in both data sets. It should be noted that TCI was comparable in importance to aspect class for the Tuttle data in the initial ordination. However, upon inspection of the results, I found that its importance was dependent on one plot that was an extreme outlier for both TCI value and high basal area for a rare species in the data set, *B. lenta*. This outlier compressed the other gradients, making interpretation of the ordination diagram difficult; removal of this plot from the ordination did not substantially change the overall result but did reduce the importance of TCI as well as improve ease of interpretation.

  Species biplots illustrate the principal similarities and differences between the two data sets (Figures 15-18). Species are arranged similarly according to their elevation optima (Figures 15, 17); notable shifts include a higher position in the Tuttle data for both *B. alleghaniensis* and *F. grandifolia*, comparable to the position of *P. rubens*. The shift of *Prunus pensylvanica* to a high-elevation optimum reflects the disturbance to *A. fraseri* forests by the balsam woolly adelgid. Species arrangements with respect to aspect class are roughly similar between the two data sets for the important species (Figures 16, 18), with more mesic species, such as *A. flava* and mesic *Acer* species, occupying higher positions. *Betula alleghaniensis* exhibits more intermediate optima for both aspect and slope in the Tuttle data. Indeed, the position occupied by this species in the Tuttle ordination is similar to the position occupied by *A. fraseri* in the Miller ordination. In the Tuttle ordination, *A. fraseri* retains a preference for north-facing aspects but now occupies primarily flatter, ridgetop slopes. *Picea rubens* has shifted from a slightly north-facing or intermediate optimum to a south-facing optimum for aspect class while maintaining an intermediate position for slope. *Fagus grandifolia* exhibits a steeper slope optimum in the Tuttle data, while *T. canadensis* and *H. tetraptera* exhibit steeper slope optima in the Miller data. In general, species positions along the slope vector are difficult to interpret
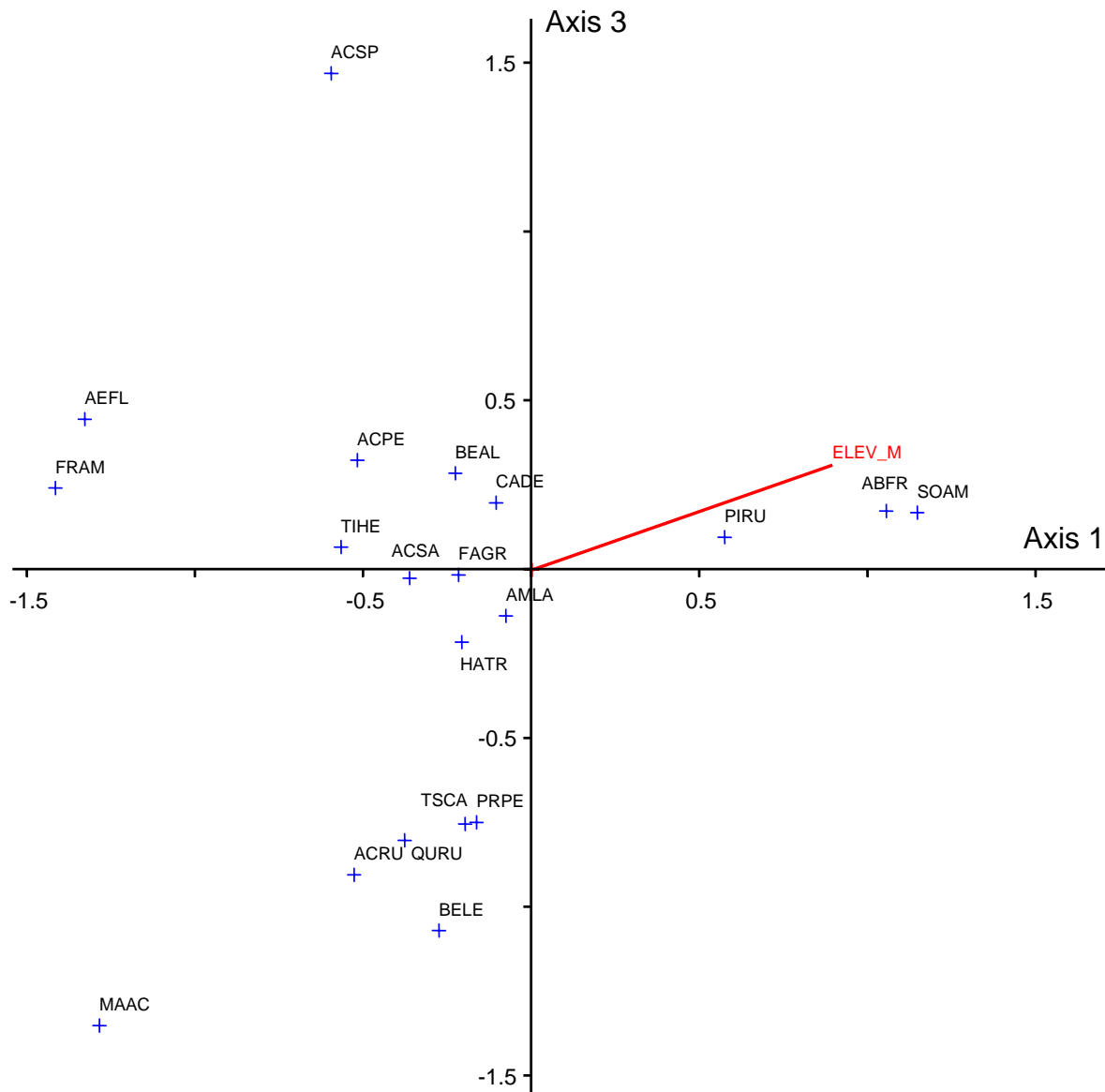
Figure 15. Canonical correspondence analysis (CCA) biplot for the Miller data, axes 1 and 3.
Species abbreviations are as in Table 3. The vector ELEV_M shows the direction and magnitude
(vector length) of correlation with increasing elevation.
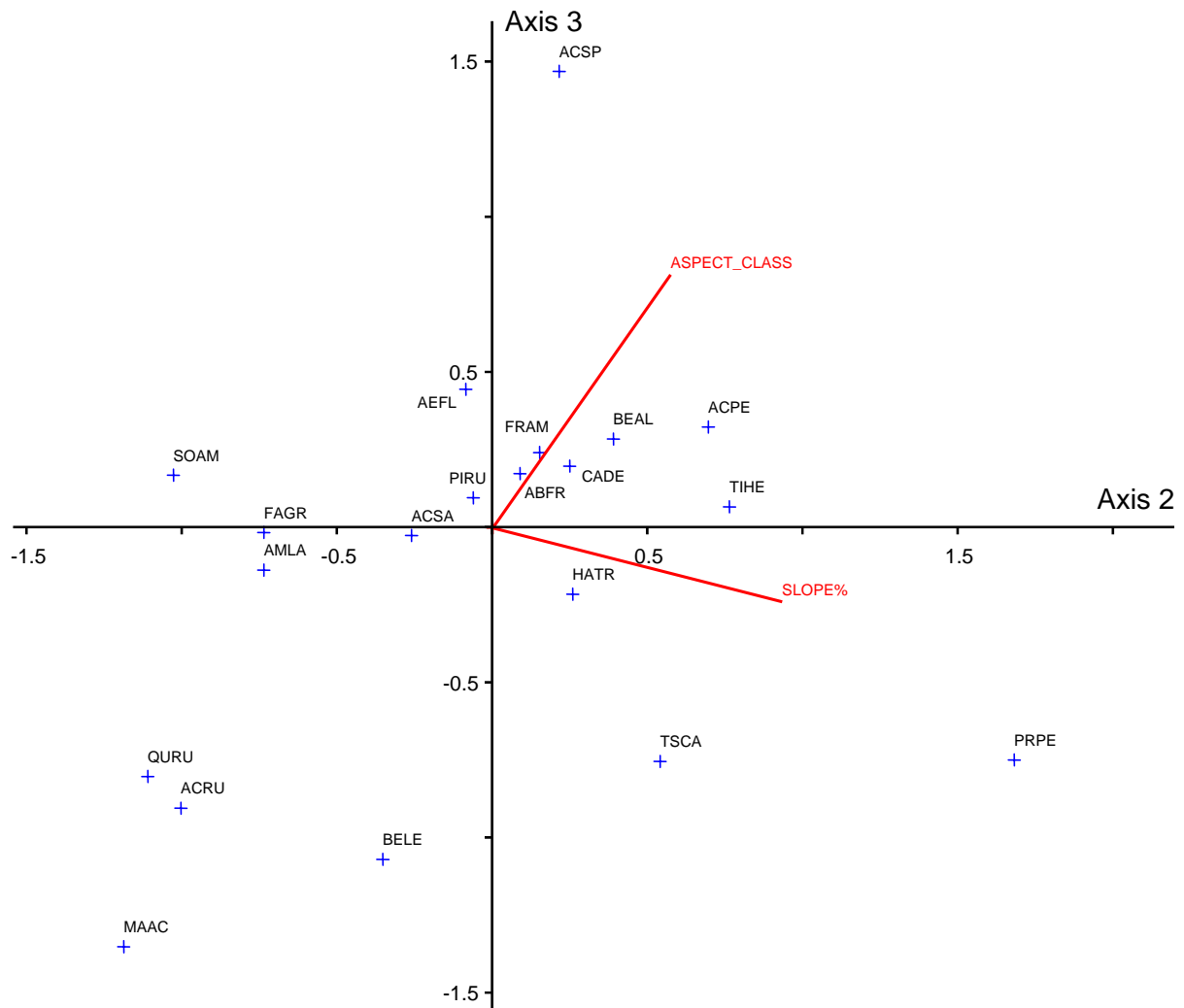
Figure 16. Canonical correspondence analysis (CCA) biplot for the Miller data, axes 2 and 3. Species abbreviations are as in Table 3. The ASPECT_CLASS and SLOPE% vectors show the direction and magnitude of correlations with increasingly northerly aspect and increasing slope steepness.

Figure 17. Canonical correspondence analysis (CCA) biplot for the Tuttle data, axes 1 and 3. The ELEV_M vector shows the direction and magnitude (vector length) of correlation with increasing elevation.

Figure 18. Canonical correspondence analysis (CCA) biplot for the Tuttle data, axes 2 and 3. The ASPECT_CLASS and SLOPE% vectors show the direction and magnitude of correlations with increasingly northerly aspect and increasing slope steepness.
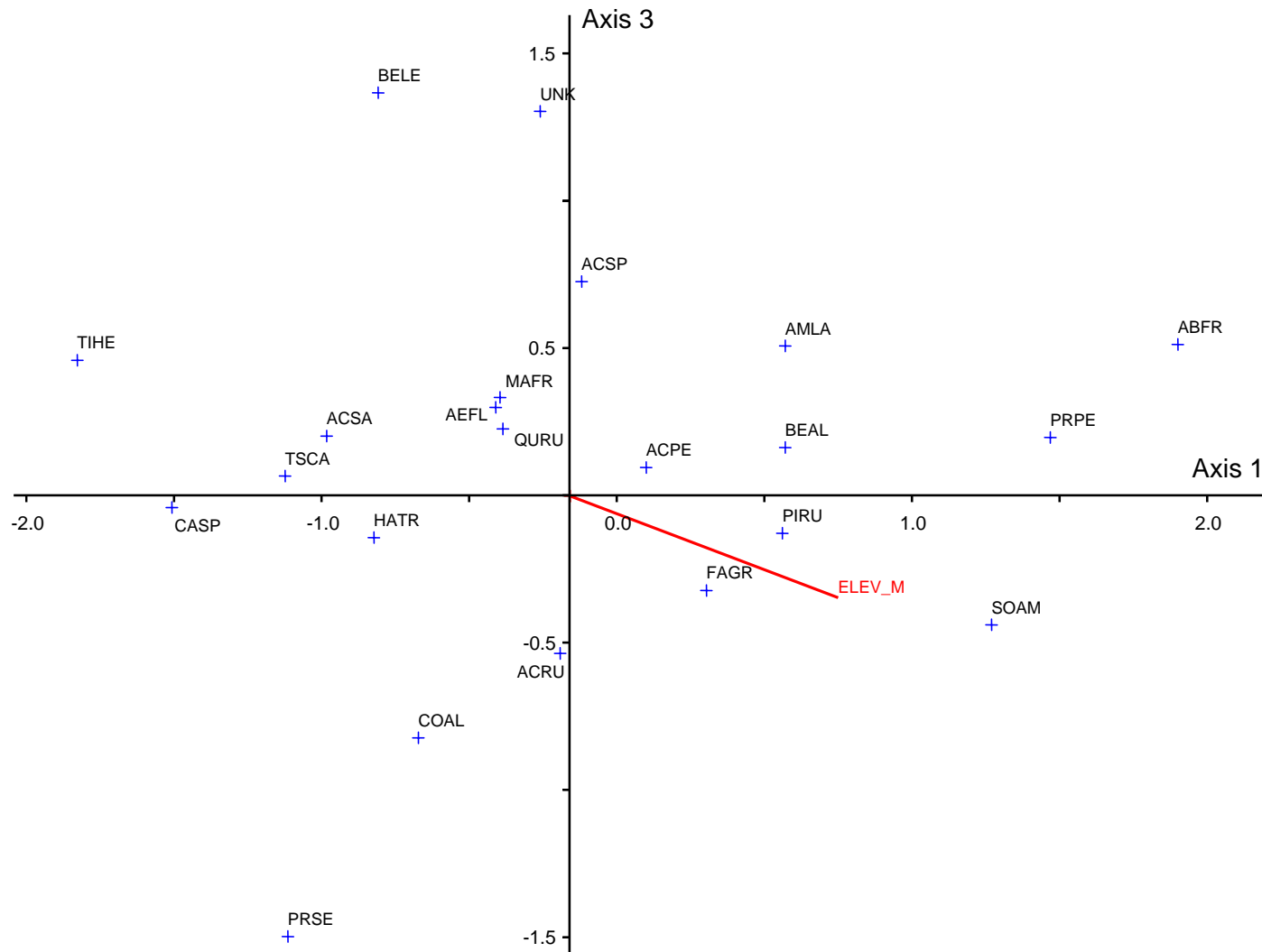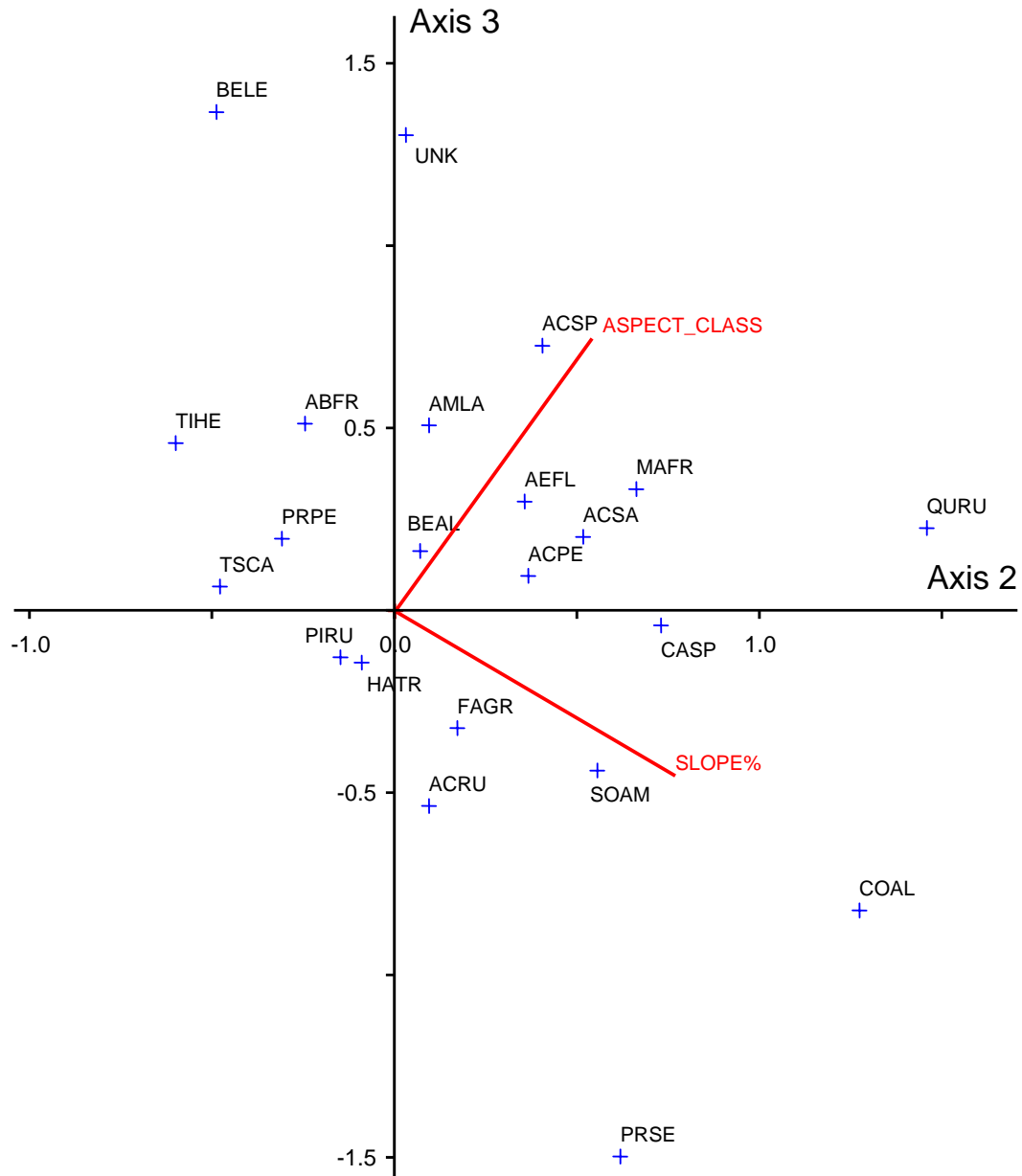
except for the widespread species mentioned above, most likely because of small overall sample

size combined with a sampling design unstratified by slope.

Chapter 5: Discussion

Ecotonal change.   Results of this study imply an ecotonal forest that is in transition,

recovering from disturbance – because of the significantly higher mean plot stem density, the

similar mean plot basal area, and higher mean plot species richness. Change in stand attributes is

most pronounced between 1400 and 1600 m elevation via increased density and between 1600

and 1700 m elevation via decreased basal area. Shifts in dominant and subdominant species

reflect primarily the most recent, acute disturbances: decimation of *Abies fraseri* by the balsam

woolly adelgid since its spread to the park in the 1960s and high mortality of *Fagus grandifolia*

from beech bark disease (*Cryptococcus fagisuga* and *Nectria* spp.) since its discovery in the park

in 1993. *Fagus grandifolia*, a formerly widespread dominant species, has been reduced to a

subdominant species, while *A. fraseri*, formerly a high-elevation dominant, is no longer even

subdominant; both species have contracted distributions. *Picea rubens* and *Betula*

alleghaniensis, mid- to high-elevation associates of both *F. grandifolia* and *A. fraseri*, not only

remain dominant but occur more frequently in plots. A low- to mid-elevation species, *Halesia*

tetraptera, has attained subdominant, widespread status, while two lower-elevation associates of

F. grandifolia, Aesculus flava and *Acer saccharum,* are not dominant or subdominant in the

Tuttle data but persist in occurrence.

Changes in size-class distributions confirm the forest recovery, showing a dramatic overall

increase in the smallest size class (10.1–30.3 cm dbh) with reductions in size class 3. Again, *P.*

rubens, *B. alleghaniensis*, and *H. tetraptera* show strong responses to the losses of *A. fraseri* and

F. grandifolia with increased density in the two smallest size classes. However, size-class

distributions imply that other low- to mid-elevation species, including *Tsuga canadensis*, *A. saccharum*, and *A. flava*, also have responded to these losses to varying degrees in the smallest size class, and *T. canadensis* notably occurs twice as frequently in plots. Strong responses of *Acer pensylvanicum*, *Acer spicatum*, and *Acer rubrum* in the smallest size class are accompanied by newly widespread distribution of these species across the ecotone. High stem densities for small, short-lived understory trees, such as *A. pensylvanicum* and *A. spicatum*, support the interpretation that these forests are actively responding to the recent acute disturbances. *Acer rubrum* and *H. tetraptera* have increased in size class 3, indicating possibly fast growth of these species as well as high survivorship into larger structural classes. In contrast, the historically more dominant canopy species (*P. rubens*, *T. canadensis*, *A. saccharum*, and *A. flava*) show apparent decreases in size class 3 accompanied by minimal change in the largest size class.

Species abundance differences by elevation illustrate important compositional changes within the ecotone. The shift to dominance by *P. rubens* still occurs between 1400 and 1500 m. However, what was once a more subtle shift – which remained complex with increasing elevation because of the mixed importance of *F. grandifolia* and *A. fraseri* – has become a more abrupt shift to dominance by *P. rubens* and *B. alleghaniensis*. Closer inspection reveals that both *P. rubens* and *B. alleghaniensis* have increased in dominance most dramatically between 1500 and 1600 m, while between 1400 and 1500 m, *P. rubens* dominance has not changed; rather, *B. alleghaniensis* appears to have replaced *F. grandifolia* in dominance, and *T. canadensis* and other hardwoods remain subdominant. Between 1600 and 1700 m, *P. rubens* has maintained its dominance through an increase in density, despite a decrease in basal area that may be attributable to increased windthrow or winter climate exposure following mass mortality of

surrounding *A. fraseri*. At the lower elevations, dominance remains a more complex assortment of *T. canadensis* and hardwoods.

Although the species structuring the four main community clusters (*P. rubens*, *B. alleghaniensis*, *T. canadensis*, and *F. grandifolia*) are the same in the two data sets, cluster composition is actually quite different between the two data sets. *Abies fraseri* has decreased in the *P. rubens* type but has slightly increased (from not present to present) in the *B. alleghaniensis* and *F. grandifolia* types. For *B. alleghaniensis*, this likely reflects increased dominance in high-elevation sites that once were dominated by *A. fraseri*. For *F. grandifolia*, this may reflect restriction of dominance to mainly higher elevation sites where *P. rubens* is codominant, whereas the typical *F. grandifolia*-mixed northern hardwood type that is most prominent in the Miller data is nearly absent from the Tuttle data, perhaps partially a result of small sample size in the lower elevations as well as transition of formerly *F. grandifolia*-dominated plots to *B. alleghaniensis*- or other hardwood-dominated plots. *Fagus grandifolia* indeed has decreased across all cluster types, including its own, except for a likely insignificant increase in the *P. rubens* cluster, although it should be noted that perhaps *F. grandifolia* responded to the loss of *A. fraseri* in both the *P. rubens* and *P. rubens-F. grandifolia* types before the onset of beech bark disease. *Betula alleghaniensis* has increased across three of the four main cluster types and has decreased in the *T. canadensis* cluster. However, this likely reflects the fact that the Miller cluster consists of *T. canadensis*-mixed northern hardwood plots, whereas the Tuttle cluster consists of high-basal-area *T. canadensis-H. tetraptera* plots with minimal representation by other northern hardwoods; these plots may represent old-growth *T. canadensis* outliers, but the subdominance of *H. tetraptera* and the presence of *A. pensylvanicum* and *A. rubrum* indicate a response to gap disturbance. The increase of *Acer* spp. (excluding *A. saccharum*) across the four

main cluster types indicates recent gap disturbances across the entire ecotone. The Tuttle *A. saccharum*-dominated plots, however, lack any obviously disturbance-related species, indicating that these may be old-growth stands unaffected by recent acute disturbances. It should be noted that while *P. rubens* still definitively dominates the *P. rubens* cluster, basal area of all conifer species including *P. rubens* has decreased while that of nearly all northern hardwood species, particularly *B. alleghaniensis* and *H. tetraptera*, has increased in this cluster.

Both direct and indirect gradient analysis support the interpretation of ecotonal reorganization, with *B. alleghaniensis* increasing at higher elevation with contraction of *A. fraseri*, *F. grandifolia* contracting to higher elevation as it declines, and *P. rubens* maintaining dominance in many plots but perhaps yielding to increased presence of northern hardwoods. Stronger correlation of Tuttle plot composition with elevation suggests that the modern ecotone is more strongly structured along the elevation gradient, and this is supported by the more pronounced dominance of *P. rubens* and *B. alleghaniensis* above 1400 m as well as decreased mean plot evenness. Further, *P. rubens*, *B. alleghaniensis*, *F. grandifolia*, and *A. pensylvanicum* now occupy similar optima along the CCA elevation gradient. *Acer rubrum* likewise has shifted to a higher-elevation optimum. While most frequently occurring species maintained similar aspect preferences (but varied in slope), *P. rubens* and *B. alleghaniensis* became polarized, with *P. rubens* dominating more frequently on south-facing aspects and *B. alleghaniensis* almost exclusively on north-facing aspects; *P. rubens*'s optimum accordingly shifted from an intermediate to a south-facing aspect, while *B. alleghaniensis*'s optimum became more intermediate but remained north-facing.

Related findings. Most studies of impacts to the high-elevation spruce-fir forests of the Great Smoky Mountains and southern Appalachians have focused within the spruce-fir-dominated

forest itself, often at the several-plot or stand level, sometimes comparing two or more widely spaced locations (e.g., Busing et al. 1988, Smith and Nicholas 1998). Many of these empirical studies have focused on *A. fraseri* mortality, regeneration, and recruitment after infestation by the balsam woolly adelgid, generally documenting overall recruitment success and persistence of *A. fraseri* following infestation, although the long-term dynamics of the balsam woolly adelgid and *A. fraseri* abundance are uncertain (Dale et al. 1991, Smith and Nicholas 2000). Harmon et al. (1983) did predict an increase in *B. alleghaniensis* in dense *A. fraseri* stands after the balsam woolly adelgid. However, Busing and Clebsch (1987) simulated stand dynamics for *P. rubens*, *A. fraseri*, and *B. alleghaniensis* and predicted that *P. rubens* would dominate upon exogenous disturbance to *A. fraseri*, whereas *B. alleghaniensis* would dominate only upon exogenous disturbance to both *A. fraseri* and *P. rubens*. Busing et al. (1988) then documented increased biomass/dominance of *P. rubens* and *decreased* biomass/subdominance of *B. alleghaniensis* at two sites above 1700 m following balsam woolly adelgid infestation but subsequently documented increased mortality of *P. rubens* from increased exposure to windthrow in the same study area in 1993 (Busing and Pauley 1994), in the absence of abnormal wind velocities or declines in radial growth of *P. rubens*. The paucity of tree species at the highest elevations and the fact that most of these studies were conducted over a decade ago limits conclusions about long-term survival of spruce-fir forests, particularly following the balsam woolly adelgid.

Another group of studies has focused on the detrimental effects of atmospheric deposition on *P. rubens* in the southern Appalachians (see McLaughlin et al. 1994 for a brief review), again focused mostly on *P. rubens* in the spruce-fir zone and often based on dendrochronological data. One of the most recent of these (Webster et al. 2004) links climate variability and regional atmospheric pollution inputs over the last century to declines in radial growth of *P. rubens* at two

GRSM spruce-fir sites at 1500 and 1800 m elevation; this same study speculates that a 1990s spike in radial growth was a response to mortality of *A. fraseri* from the balsam woolly adelgid. These studies do not document increased mortality directly from atmospheric inputs and are not integrated with studies of similar effects on co-occurring species, so again, the results are inconclusive regarding the long-term survival of *P. rubens* in spruce-fir forests.

While the intention of this study is to document ecotonal change over 70 years as an additional route to evaluating persistence of high-elevation spruce-fir forests in GRSM under multiple impacts, the results seem to capture primarily the effects of recent declines in two ecotone-related species, *A. fraseri* and *F. grandifolia*. This likely masks any changes occurring between the 1930s and 1970s as well as changes from other ongoing impacts. Ecotone-focused studies from the intervening time period would be useful but are scarce, with three exceptions: 1) Schofield (1960) collected plot data in ecotonal transects for 10 ecotonal "types", including "virgin", cut, and burned areas. Schofield's study included sites with dense *Rhododendron maximum* understory, and he considered *P. rubens*-dominated sites ecotonal. However, although only anecdotally comparable, his results echo site preferences found for several species in the Miller data (Busing et al. 1993) and Tuttle data: Across "types", *P. rubens*, *F. grandifolia*, and *T. canadensis* attained consistently higher basal area on southern slopes, whereas *Betula alleghaniensis* basal area was higher on northern slopes. However, *A. fraseri* also attained consistently higher basal area on southern slopes, in contrast to the north-facing site preference found in the Miller and Tuttle samples of this study. Also of interest, *B. alleghaniensis* basal area was greater on slopes with evidence of cutting, while *P. rubens* and *F. grandifolia* basal area was lower on these sites. Schofield observed that the ecotone occurred at higher elevation on south-facing slopes, which he attributed to cutting and burning. 2) DeSelm (1970s) collected

plot data along elevational transects in the westernmost ecotonal watersheds of GRSM but did not publish results of any analysis. 3) More recently, Hayes (2002) used a remotely sensed map of GRSM spruce-fir extent (date not specified) and Pyle's (1984) logging history map to investigate the interactive effects of logging history, aspect, and potential insolation on spruce-fir presence in a 1-km buffer straddling the boundary of the spruce-fir zone. His results suggested that the mean elevation of sites with spruce-fir present was higher on logged south-facing slopes.

   Perhaps more useful are studies of GRSM forest types related to the ecotone, such as northern hardwood cove, *T. canadensis*, and *F. grandifolia* forests, particularly those studies investigating change over time using the Miller or other historical data. Busing (1989) resampled two of Stanley Cain's 1935 cove hardwood plots (Cain unpublished in Busing 1989), sampled approximately five years after mortality of *Castanea dentata* from chestnut blight (*Cryphonectria parasitica*) at both sites. Total stand and *A. saccharum* basal area increased at both sites, and either *T. canadensis* or *H. tetraptera* increased in basal area at each of the sites; these results are similar to the findings of Woods and Shanks (1959) in their study of post-blight forest dynamics in GRSM. In 1998, Knebel (1999) approximately relocated and resampled 20 Miller *T. canadensis*-dominated plots, including some plots between 1200 and 1500 m elevation. She found that while *T. canadensis* sapling density remained the same over the 60 years, *T. canadensis* basal area and density decreased overall, especially in the larger size classes. As in my results, species such as *A. pensylvanicum*, *H. tetraptera*, and *A. rubrum* dramatically increased in sapling densities and overall importance. Similar dramatic increases in *F. grandifolia* sapling density and importance indicate that Knebel's plots had experienced little to no mortality from beech bark disease at that time. Knebel attributed these changes primarily to the reduction of *C. dentata* frequency from six to zero of the 20 plots. In contrast, Jenkins

(personal communication 2006) commented that *T. canadensis* had increased in the understory in the park as a result of fire suppression, although fire was likely uncommon at the higher elevations in the eastern park.

Finally, between 2000 and 2004, Vandermast (2005) sampled high-elevation *F. grandifolia* forests to compare to both *F. grandifolia* forests in the Miller data and in 1970s plots. He found increases in non-diseased, co-occurring northern hardwood species and *P. rubens*, particularly in the smallest size classes, similar to my results and likely indicating release following mortality of *F. grandifolia* from beech bark disease. He noted a decline in overall *A. flava* abundance similar to my results. The striking finding in his study was greater abundance of *F. grandifolia* in the 1970s plots compared to the Miller plots and, surprisingly, abundance similar to that of the Miller data in 2000-2004; he concluded that *F. grandifolia* forests had been aggrading since the 1930s and then had declined with the onset of mortality from beech bark disease.

Summary of impacts and consideration of future dynamics. While the results of this study suggest recovery and reorganization of ecotonal stands, most obviously from the recent losses of *A. fraseri* and *F. grandifolia*, direct causes are by no means easily mapped onto the effects shown here and are not the intent of this study. Vandermast's study (2005) deftly illustrates the likelihood that the recent changes observed (or not) in the ecotone are masking other compositional and structural changes that had occurred since the 1930s and that may continue or interact with the observed changes. For example, the findings of Busing (1989) and Knebel (1999) support the possibility that some changes in the ecotone since the 1930s are attributable to recovery from chestnut blight; indeed, inspection of the Miller data reveals unlogged, unburned *C. dentata*-dominated plots between 1200 and 1700 m in the study area watersheds that were

excluded from comparison as non-northern hardwood plots (or perhaps plots that did not border any spruce-fir forest).

In the case of the diverse range of community and site types encompassed by the ecotone, current forest composition may reflect different stages of impact and recovery from a long list of direct, discrete impacts, including release from selective cutting and grazing; fire suppression; removal of *C. dentata* by chestnut blight; increased exposure to windthrow from the onslaught of canopy openings; seedling, root, and soil disturbance by non-native wild boars (present in the eastern park for the past 10-15 years; Peter White, personal communication 2006); and the usual array of natural disturbances such as hurricanes, flooding, and ice storms. Ongoing, continuously distributed impacts further complicate investigation of change: Atmospheric deposition may affect health of ecotonal species directly through foliar damage from ozone or indirectly through biogeochemistry (McLaughlin 1994). Recently documented climate change, whether transient or a long-term trend, can alter both the dominant environmental gradients (temperature and precipitation) and the disturbance gradients that structure these montane forests (Harmon et al. 1983). Webster et al. (2004) found a recent shift in long-term temperature-precipitation data for GRSM from cycles of warm/wet and cool/dry to warm/dry and cool/wet. Anchukaitis et al. (2006) support this through a finding of increased drought sensitivity of southern Appalachian conifers as recorded in tree rings. An impending decline in *T. canadensis* upon full infestation of GRSM by the hemlock woolly adelgid (*Adelges tsugae*) will impose yet another cycle of targeted mortality and canopy openings on the ecotone. The spatial and temporal extents of these factors overlap, and processes likely interact (e.g., the effect of temperature-precipitation cycles on dynamics of the hemlock woolly adelgid).

With such complexity, what can be said about the GRSM deciduous-coniferous ecotone? Based on the results of this study, the abundance and distribution of *P. rubens* seem at least preserved in the ecotone, pending success of enough of the abundant small trees. *Abies fraseri* appears to be persisting in a diminished state at the highest elevations. It is unknown whether *B. alleghaniensis* will persist in dominating former *A. fraseri* forests, particularly on north-facing slopes. Perhaps *P. rubens* will survive under protection of the *B. alleghaniensis* canopy and succeed to dominance. However, in the meantime, if drought stress begins to induce mortality, *P. rubens* could diminish on the south-facing aspects it now dominates. One can also envision an assortment of exogenous stressors upon *P. rubens* that could combine to result in increased mortality, reduced suppression tolerance, or reproductive/establishment failure, perhaps leading to widespread decline. Such stressors may affect other ecotonal species, too, however. The perceived increase in this study of northern hardwood species in *P. rubens*-dominated stands may indicate a transition in progress. *Picea rubens* and/or *A. fraseri* already may be persisting in GRSM beyond their respective climate or competitive envelopes, as perhaps evidenced by the near-restriction of *A. fraseri* to north-facing, high-elevation slopes above 1500 m elevation, when the species formerly showed, in the Miller data, a slight affinity for north-facing sites but was abundant on both aspects. In contrast, *P. rubens* may expand at the expense of another species if it benefits from release on *T. canadensis* sites affected by the hemlock woolly adelgid.

Is the GRSM spruce-fir ecotone important? Time will tell, and this study may contribute to longer term research and monitoring of the *entire* ranges of *P. rubens* and *A. fraseri* in GRSM. A wish list for future study of the GRSM spruce-fir ecotone could include a more complete sample of the ecotone, including *Rhododendron* species-dominated sites and stratification by land use/disturbance history; the establishment of physically marked permanent plots to

accompany GIS coordinates for more reliable repeat sampling; attempted relocation of historical

plots; and the collection of more site and vegetation data (e.g., tree cores for dendroecological

analysis). It seems feasible that understanding the prospects for *P. rubens* and *A. fraseri*

persistence in the face of exogenous stressors could inform conservation efforts. For example,

this study's finding of *A. fraseri*'s current near-restriction to north-facing sites above 1500 m

may mean limited re-expansion pathways should surviving *A. fraseri* forests fully recover from

the balsam woolly adelgid. Likewise, this knowledge could inform site selection for spruce-fir–

related research, conservation, or restoration projects. Beyond conservation in GRSM and this

study in particular, attempting to unravel montane deciduous-coniferous ecotonal dynamics may

forward our understanding of complex ecological dynamics in the context of global change.

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