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Measuring spatial and temporal shifts in forest structure and composition in high elevation beech forests in response to beech bark disease in Great Smoky Mountains National Park



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ABSTRACT

Exotic forest pests and pathogens are among the most serious environmental threats to millions of hectares of forested land worldwide. Beech Bark Disease (BBD) is a non-native, pathogenic complex consisting of associations between scale insects and fungi. First confirmed in Great Smoky Mountains National Park (GRSM) in 1986, this complex has since threatened local high elevation beech forests, which are G-1 ranked (critically imperiled) forest communities where American beech (*Fagus grandifolia* Ehrh.) is a foundational tree species. In 1994, GRSM initiated the BBD Monitoring Protocol at 10 high elevation beech forest plots in the Park. The plots were sampled biennially from 1994 to 2012 and again in 2017 to investigate infestation patterns and host mortality. Permutational multivariate analysis of variance (PERMANOVA) and nonmetric multidimensional scaling (NMDS) techniques were used to investigate shifts in forest structure and composition over the 23-year study period. Species-specific changes were analyzed using repeated measures linear mixed effects models (RMLMM). High elevation beech forest communities are changing through time with trajectories becoming more influenced by *Acer* and *Betula* species. Despite great variability in plot location, aspect, slope, and beginning species composition, time was a significant factor, explaining ~10% of the variation in relative basal area. Species-specific shifts were highly variable. While overstory *Fagus grandifolia* basal area declined significantly over the 23-year study period, no significant change in total basal area was observed, indicating that the loss of these mature trees was compensated by co-occurring species. Understory sapling and woody seedling abundance of *F. grandifolia* increased relative to most other species in the study. The loss of the foundational species, *F. grandifolia* (the dominant tree species which defines high elevation beech forests), will have broad consequences for associated biota, ecosystem function, and potentially, the long-term persistence of high elevation beech forests in GRSM.

1. Introduction

Exotic forest pests and pathogens are among the most serious environmental threats to millions of hectares of forested land across the United States (Castello et al., 1995; Karel and Man, 2017). They are now present in all forest ecosystems (Castello et al., 1995), often as a result of human introduction (Cappaert et al., 2005; Ellison et al., 2005; Dodds and Orwig, 2011; Giencke et al., 2014). Forest pests and pathogens drive both short- and long-term changes in forest composition,

forest structure, and ecosystem-level processes (Lovett et al., 2006). While distinctions between the two are somewhat arbitrary, short-term effects (e.g., chlorosis, defoliation, loss of vigor, crown dieback, or even premature tree death) are more easily observed as a direct result of the pest or pathogen, while long-term effects are more difficult to quantify. Long-term effects (e.g., spatial and temporal shifts in forest structure and composition, influence on nutrient cycling processes, loss of biodiversity, shifts in ecosystem function, and contributions to climate change) can have both direct and indirect consequences over many

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years, decades, or centuries (Lovett et al., 2006; Cale et al., 2017).

In the eastern United States, forests have frequently experienced destructive forest pests and pathogens, all of which have altered forest structure and composition over both spatial and temporal scales. While the deleterious effects on an individual tree can lead to early tree death, the impact on the species is further exacerbated when species cover wide distributional ranges—leading to a cascade of indirect effects across the forest landscape. This has been seen with the beech bark disease (BBD) complex since its accidental introduction into North America more than 100 years ago.

1.1. Beech bark disease

Beech bark disease is a non-native pathogenic complex afflicting *Fagus grandifolia* Ehrh. and consists of both an insect and a fungal component. Two insects, the non-native beech scale (*Cryptococcus fagisuga* Lind.), and the native American beech scale (*Xylococculus betulae* Perg.) both feed on beech stems of all sizes (Shigo, 1972; Cale et al., 2017). Feeding wounds produced by both insects predispose beech stems to subsequent fungal infections by either *Neonectria faginata* (Pers.:Fr.) Fr. Var. Lohman, A. M. Watson, & Ayers or *Neonectria ditissima* (Tulasne & C. Tulasne) Samuels & Rossman, which are both hypothesized to be native to North America (Wiggins et al., 2004; Cale et al., 2015; Castlebury et al., 2006). Combined, the BBD complex has led to extensive mortality of *F. grandifolia* trees, decreases in net forest productivity, and decreases in biodiversity throughout eastern North America (and Canada) for more than a century (Cale et al., 2017).

Shigo (1972) described BBD as having three, biologically-recognizable stages that afflict beech forests over time—the advancing front, the killing front, and the aftermath stage. The advancing front is characterized by low-levels of baseline *F. grandifolia* mortality; the killing front is characterized by extensive tree dieback and above-ground tree mortality and the aftermath stage is recognized by *F. grandifolia* trees in various stages of decline—from small canker development (of collapsed parenchyma cells; Koch et al., 2010) to extensive tree dieback and death. Following the aftermath stage, as host tree populations decline, scale populations, *Neonectria* species abundance, and tree mortality all decrease while beech thicket formation (via root sprouting) can increase (Giencke et al., 2014). Any trees that survive the aftermath stage will exhibit chronic stress (as a result of abundant canker development) and up to 40% less radial growth (Gavin and Peart, 1993).

The BBD complex was first observed in Europe in the mid-1800's on European beech (*Fagus sylvatica* L.; Wiggins et al., 2004; Castlebury et al., 2006), and by 1972, the disease had a 100% occurrence in beech forests throughout Europe (Shigo, 1972). The first outbreaks in North America were reported in Bedford, Nova Scotia, in 1911 (Ehrlich, 1934). The complex is thought to have arrived in Halifax, Nova Scotia, circa 1890 on stocks of ornamental European beech trees (Wiggins et al., 2004). While the scale component of the complex is considered non-native, phylogenetic relationships now suggest that the fungal component is actually native to North America (Castlebury et al., 2006).

From Nova Scotia, the disease spread south relatively quickly. Non-native beech scale (*C. fagisuga*) populations were discovered in 1929 at Arnold Arboretum (Harvard University, Boston, MA), and were thought to be approximately 10-years old at that time (Ehrlich, 1934). As reviewed in Houston (1994), BBD then made its way into Pennsylvania by 1958, continuing to spread south into West Virginia by 1981, west into Ohio by 1984, and finally, Michigan by 2000. As of 2016, BBD could be found in 15 states, with the furthest reaches extending west of the Great Lakes into Wisconsin, and south into Tennessee and North Carolina—and subsequently, high elevation beech forests of Great Smoky Mountains National Park (GRSM; Wiggins et al., 2004; Cale et al., 2017).

1.2. High elevation beech forests of Great Smoky Mountains National Park

GRSM is one of the largest expanses (211,415 ha) of protected forest in the eastern United States (National Park Service, 2011). The Park is both an International Biosphere Reserve and a World Heritage Site due to its biological importance and diverse biological communities (Jenkins, 2007).

In the Park, high-elevation deciduous hardwood forests extend to elevations of 1680 m (Whittaker, 1956). These deciduous hardwood forests are comprised of four primary forest types: northern hardwood forests, high-elevation oak forests, forested boulderfields, and high elevation beech forests—combined, these forest types cover ~ 17% of the Park (34,109 ha; Jenkins, 2007). High elevation beech forests are defined as near monoculture stands of *F. grandifolia* trees at relatively high elevation usually found on south-facing slopes, and were historically called beech orchards by the locals (Russell, 1953).

While *F. grandifolia* covers a wide range of elevations in GRSM (473 m at Grassy Branch to 1781 m at Sweat Heifer), there are few of these high-elevation beech forests (above 1524 m, as per Russell's definition) in the Park (Ward, 1986; Blozan, 1995). Ashe (1922) estimated these forest types equate to less than 4000 ha in North Carolina, and probably less in Tennessee. Due to their restricted range, infrequent occurrence, and limited distribution across the Southern Appalachian Mountains, high elevation beech forests have been designated as G1-ranked (critically imperiled) forest communities since 2002 (NatureServe, 2018). Putting these communities in further peril, is the influx of both BBD (Ward, 1986) and hog rooting by the exotic European wild boar (*Sus scrofa* L.; Bratton, 1975). Combined, these two, large-scale disturbances have resulted in a forest community that is at risk of possible extinction (NatureServe, 2018).

1.3. Exotic pests and pathogens in Great Smoky Mountains National Park

BBD was first confirmed in GRSM in 1986, though its timing of arrival, range, and severity in the Park at the time were unknown (Ward, 1986; Taylor, 2012). This pathogenic complex has since spread throughout local high elevation beech forests in the Park, leading to the loss of mature *F. grandifolia* trees within these habitats (Russell, 1953; Wiggins et al., 2004). While the effects of BBD are well documented in the northeast (see Cale et al., 2017), the direct and indirect effects on forest structure and composition, and ecosystem integrity in GRSM are not as well documented (Russell, 1953; Oh, 1964; Wiggins et al., 2004; Tuttle, 2007). Following the confirmation of BBD near Newfound Gap in 1986, the *BBD Monitoring Protocol for GRSM* was established by the National Park Service in 1994 to monitor and document patterns of infestation, progression, and host mortality in 10 high elevation beech forests throughout GRSM (Blozan, 1995; Taylor, 2006).

1.4. Summary and objectives

Fagus grandifolia has been threatened by BBD since its accidental introduction into North America nearly a century ago, and GRSM now represents a large portion of the complex's southernmost distribution (Ward, 1986; Houston, 1994). In GRSM, long-term data have been collected biennially since 1994 on BBD and its effect on forest structure and composition in 10 plots established within these high elevation beech forests. Over the course of 23 years, it is likely that these plots have experienced shifts in species composition, frequency, density, and basal area. While beech mortality can be a slow process of decline over many years, the need for continued research of long-term data sets from these permanent monitoring plots can help provide a better understanding of the viability of these critically imperiled forest ecosystems.

The goal of this study is to investigate how BBD (and the subsequent death of mature *F. grandifolia* trees) has influenced spatial and temporal shifts in forest structure and composition in 10 high elevation beech forests established by GRSM. Using spatial and temporal data collected

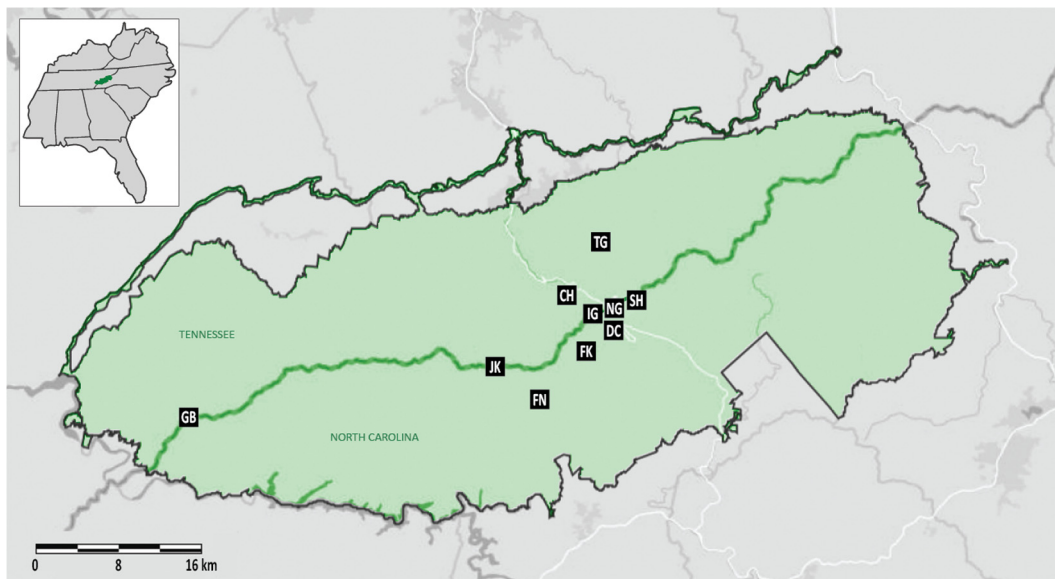


Fig. 1. Location of 10, long-term, high elevation beech forest monitoring plots in GRSM. Black dots represent plot location within the Park. Plot details are given in Table 1. SH = Sweat Heifer; JK = Jenkins Knob; FN = Forney Ridge; TG = Trillium Gap; DC = Deep Creek; IG = Indian Gap; CH = Chimneys; FK = Fork Ridge; NG = Newfound Gap; GB = Gregory Bald.

in GRSM high elevation beech forests since 1994, the goal was to assess (1) overstory tree shifts community structure and composition in GRSM high elevation beech forests 2) the influence on understory saplings and woody seedlings, and (3) the future direction of high elevation beech forests in GRSM.

2. Materials and methods

2.1. Field sampling

2.1.1. Plot establishment

In 1994, 10 permanent 20 m × 20 m (400 m² [or 0.04 ha]) plots were established in select high elevation beech forests throughout GRSM (Fig. 1). These 10 plots (Table 1) were sampled biennially from 1994 to 2012 by GRSM Park staff to monitor populations of *F. grandifolia* for BBD infestation, progression, and host mortality (Taylor, 2006). Plot coordinates may be obtained through a formal request to

Table 1
GRSM long-term high elevation beech forest monitoring plot characteristics¹.

Plot name	Plot number	Number of <i>F. grandifolia</i> ²	Scale Density ³	Elevation (m)	Aspect
Sweat Heifer (SH)	01	28	high	1781	SE
Jenkins Knob (JK)	03	54	low	1654	N
Forney Ridge (FN)	04	77	high	1530	W
Trillium Gap (TG)	06	55	none	1435	W
Deep Creek (DC)	07	31	none	1411	S
Indian Gap (IG)	09	55	low	1625	S
Chimneys (CH)	10	20	low	1125	NW
Fork Ridge (FK)	14	35	high	1495	S
Newfound Gap (NG)	16	49	low	1584	S
Gregory Bald (GB)	17	45	none	1412	N

¹ Plot characteristics as defined in 1994 for 10, permanent 20 m × 20 m (400 m²) long-term high elevation beech forest monitoring plots in GRSM. Table data are from Taylor (2006).

² Number of overstory *F. grandifolia* trees in each plot greater than 3.5 cm DBH at time of plot installation (1994).

³ Estimate of scale density in plot at time of plot installation in 1994 (none = scale not found; low = newly established populations; high = well-established populations). Data are from Taylor (2006).

the Park Service. Each plot was selected in 1994 based on the criteria of having at least 20 *F. grandifolia* stems greater than 3.5 cm DBH (Millers et al., 1992). At the time of plot establishment, plots were ranked for scale density (none, low, or high; Table 1), and all tree species within the plot greater than 3.5 cm DBH were tagged with numbered aluminum tags. In subsequent years, any new trees with growth exceeding 3.5 cm DBH were tagged as new trees during the study period. Dead trees were measured until the tree fell, or until the tag had fallen from the tree, at which point the trees were excluded from subsequent data collection.

Between July and September of 2017, all 10 plots were resampled following the BBD Monitoring Protocol for GRSM (with modification; Taylor, 2006). For the 2017 resampling, all field metrics were collected by the author, an 8-year International Society of Arboriculture (ISA) Certified Arborist (Rumble SO-6435A). Due to time and/or sampling restraints, no new trees were tagged nor were data collected for scale insects or fungal associations, since the latter requires twice yearly monitoring (once in spring/summer and once in fall/winter) due to the life stage of each organism (Wiggins et al., 2004). Any evidence of scale insects or fungal infection observed on trees within plots was documented but were not formally quantified.

2.1.2. Overstory tree sampling

In 2017, within each plot (400 m² total sample area per plot; Fig. 2), all previously-tagged overstory trees greater than 3.5 cm DBH were sampled and listed as live or dead. Crown position classification (i.e., crown class) was defined for each live tree as: suppressed (S), intermediate (I), co-dominant (CD), or dominant (D) following Smith (1962). Crown dieback was only evaluated by Rumble (SO-6435A) to maintain consistency, since crown dieback techniques described in the GRSM protocol require two field technicians be trained following the USFS Crown Condition Rating Guide (Taylor, 2006). Live and dead tree dieback classification (as determined by the loss of upper canopy due to tree decline or death) follow Taylor (2006) and were assigned to one of six classes: no dieback (0), 0–10% dieback (1), 11–50% dieback (2), greater than 50% dieback (3), recently dead (fine twigs present; 4) or long dead (fine twigs absent; 5). Crown defoliation (as determined by the loss of leaf area caused by insect feeding) was evaluated in the same manner as in the six tree dieback classes described above in 2.1.2.

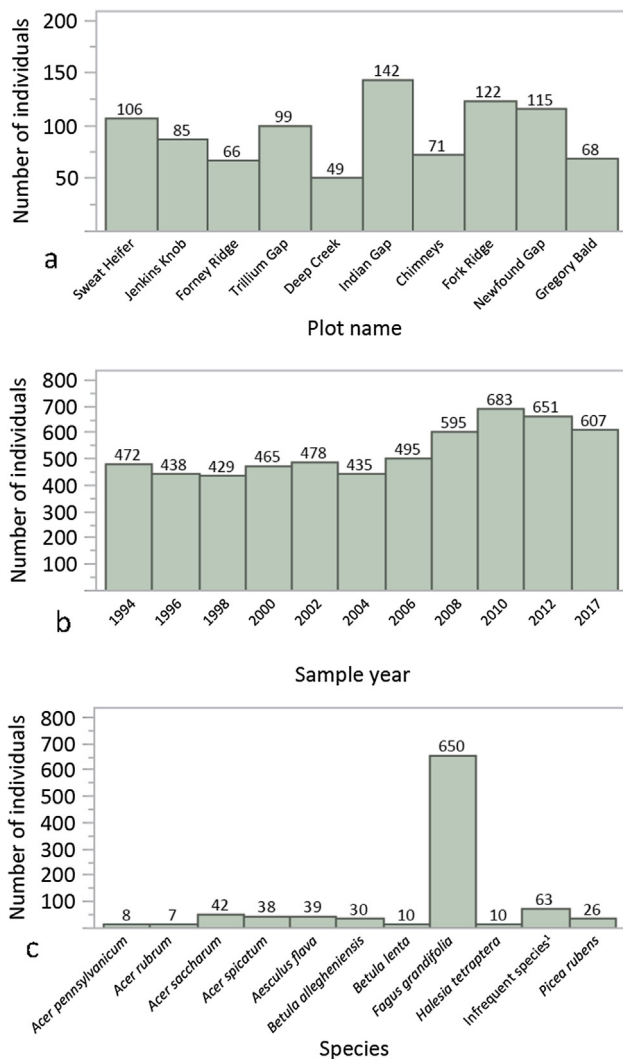


Fig. 2. Abundance and distribution of live, overstory trees observed ($n = 923$) across 10 long-term high elevation beech forest monitoring plots over the 23-year study period (1994–2017). Data organized by plot name (a), by sample year (b), and by species (c). Note y-axis scales vary across Fig. 2a, b, and c. ¹Infrequent species includes analysis of the 10 overstory tree species not identified in at least three plots (see Table 2).

2.1.3. Understory sapling sampling

In 1994, each plot was further divided into four, 10 m × 10 m subplots (Fig. 2). Three of the four subplots were randomly selected at that time to monitor understory sapling regeneration characteristics over time. Within each of these three subplots, a single nested 2 m × 8 m strip (Fig. 2) was selected (and defined in the GRSM protocol) for recording understory saplings (i.e., saplings that exceeded 1.37 m in height, but were less than 3.5 cm DBH). These same three, predefined strips (48 m² total sample area per plot; Fig. 2) were sampled within each subplot by GRSM Park staff biennially (1994–2012). In 2017, at each plot, these same three, predefined strips were sampled recording species, live or dead status, and basal diameter (measured with dial calipers 15 cm from ground level).

2.1.4. Woody seedling sampling

Nested further within each of the three 2 m × 8 m strips described above in 2.1.3., a single 1 m × 1 m quadrat (Fig. 2) was randomly selected in 1994 (and defined in the GRSM protocol) to monitor woody seedling germination characteristics over time. The same three, predefined quadrats (3 m² total sample area per plot; Fig. 2) were sampled

within each strip by GRSM Park staff (biennially 1994–2012). In 2017, at each plot, these same three, predefined quadrats were sampled, recording species, live or dead status, and all identifiable woody seedlings were tallied, assigning them to one of five size class categories: number of germinals (i.e., newly emerged seedlings; [1]), number of 1- to 4-year old plants (determined by counting growth nodes on the main stem of the plant; [2]), number of 4-year old to ¼ m-tall plants [3], number of ¼ m- to 1 m-tall plants [4], and number of plants greater than 1 m tall [5].

Within high elevation beech forests, thicket formation of *F. grandifolia* seedlings is common and clonality has been observed at some sites (Morris et al., 2014). However, the present study does not attempt to answer the question of the source of these new *F. grandifolia* woody seedlings. To clarify which reproductive mechanisms is driving potential thicket formation in GRSM, further molecular analyses would likely be required.

2.2. Data analysis

All data generated and provided by GRSM (1994–2012), plus field data collected in 2017 were compiled, organized, and inspected for quality control prior to analyses. Any measurements recorded for dead-standing overstory trees, dead understory saplings, or dead woody seedlings were removed prior to all summaries and analyses, such that only live tree measurements were analyzed. Abundance and distribution summaries were conducted by plot, by sample year, and by species in JMP® 14 (SAS Institute, Cary, NC) separately for (1) overstory trees, (2) understory saplings, and (3) woody seedlings.

2.2.1. Overstory trees basal area calculations

To calculate each tree's BA, its DBH (cm) must be first converted to a cross sectional area (m² tree⁻¹) by use of the foresters constant (Husch et al., 1982). Basal area is defined as a cross sectional area of a tree that has been measured at DBH (Husch et al., 1982). Since BA is directly related to stand volume and can be a good measure of stand density, conversion of DBH measurements to BA is a frequent and useful practice in forest research, allowing for the comparison of a species dominance within and across forest types (Husch et al., 1982). BA per hectare values were then calculated by dividing each tree's BA by the total plot area sampled (0.04 ha). These BA per hectare values were used in all subsequent summaries and analyses for overstory tree data to allow for comparisons across other forestry studies.

Overstory tree BA per hectare data were sorted to calculate the sum of BA per hectare by year, for each species across all plots, the sum of BA per hectare by year, for each plot, and the sum of BA per hectare by year, for each species in each plot. To obtain relativized BA per hectare values for each species within a plot, the sum of that species yearly BA per hectare value was divided by the total BA per hectare value of all species in the plot, for that year.

2.2.2. Overstory trees community-level analyses

Using each species' relativized overstory tree BA per hectare data, a 'community observation × species matrix' was constructed to include all plots and all sampling years ($n = 110$; i.e., 10 plots × 11 sampling years; McCune and Grace, 2002). Four community observations were removed from this matrix due to evident experimental errors in field sampling (e.g., Forney Ridge and Indian Gap only had *F. grandifolia* data represented in 1996 and 1998, respectively, while numerous other species were represented in the preceding and subsequent years), Chimneys was missing all overstory tree data for 2004, and Sweat Heifer had an obvious, inaccurate DBH measurement for an *A. spicatum* tree that was sampled in 2006. This resulted in a matrix containing 106 community observations ready for analysis.

To investigate spatial and temporal shifts in community composition (i.e., which species are decreasing or increasing in relative BA per hectare) over time, a permutational multivariate analysis of variance

(PERMANOVA; Anderson and Walsh, 2013) was conducted. This analysis is based on Bray Curtis dissimilarities for all pairwise comparisons between community observations (Anderson and Walsh, 2013). Bray Curtis dissimilarities range from 0 to 1 (where 0 indicates no similarities between two communities and 1 corresponds to compositions that match exactly). Because multivariate analyses can be biased by extremely rare species (McCune and Grace, 2002), only species identified in at least three plots are included. Species not identified in at least three plots were combined and analyzed as infrequent species in the PERMANOVA analysis.

All data were analyzed in R v3.1.1 (R Core team, 2017). The PERMANOVA was conducted using the function 'adonis' (in the 'vegan' package) to analyze the 'community observation × species matrix' as a function of both time and plot, with multiple observations nested within plot. The PERMANOVA was set to run 10,000 iterations to test the observed relationships against randomized data. This model looked at both time and plot as main effects, as well as the interaction of the two (i.e., time, plot, and time × plot).

To visualize the PERMANOVA results, non-metric multidimensional scaling (NMDS) techniques were employed in R using the function 'metaMDS' (in the 'vegan' package) to assess shifts in community composition (i.e., which species are decreasing or increasing in relative BA) over time. The NMDS is a multivariate representation of all dissimilarities (of a species) for every time point and every plot, of which was constrained to two axes (for ease of interpretation). NMDS is similar to principal component analysis (PCA), but instead uses ranks to test the dissimilarities of the relativized data (McCune and Grace, 2002). By using ranked data, the NMDS avoids bias that commonly occurs when using PCA, which assumes multivariate normality (Johnson and Wichern, 2007). This assumption is often violated in temporal ecological datasets (Clarke and Grant, 1968; Norden et al., 2007; Ramage et al., 2012), and was true for this dataset, thus the NMDS was used as a visualization tool. The NMDS stress value of 0.14 (i.e., 14%) offers a "fair" representation of community change as noted by Kruskal (1964) who describes stress values as positive, dimensionless numbers that can be expressed as percentages. This is effectively our measure of goodness of fit, whereby lower stress values indicate better fit.

2.2.3. Overstory trees species-specific analyses

Following the community-level analysis, absolute overstory tree data was used to evaluate species-specific shifts in BA per hectare over time with repeated measures linear mixed effects models (RMLMM) using the function 'Anova' (in the 'nlme' and 'car' packages). A secondary generalized least squares (GLS) model (function 'gls' in the 'nlme' package) was used for post-hoc visualization of the results. Both models were employed for each of the species identified in at least three plots, however, only the results from the RMLMM are reported. For the remaining species not identified in at least three plots, these species were combined and analyzed as infrequent species. Lastly, total BA was analyzed using the combined data of the two categories.

The RMLMM model uses time as a fixed factor, and plot as a random factor (allowing each plot to have a random intercept). Continuous autocorrelation structures (function 'corCAR1' in the 'car' package) were applied to both models using BA per hectare as the response variable and time as the continuous covariate (i.e., the question of interest). Autocorrelation structures were required because data were repeatedly sampled, and observations were not independent through time.

For each of the analyses, residuals were assessed visually to check for normality. Based on the asymmetry of the residuals, three species, *Acer pennsylvanicum* L., *B. lenta*, and *P. rubens* were natural log transformed to meet model assumptions. Zero values were removed from the analysis for *B. lenta* because it did not show up until late in the timeline. The same data used for the PERMANOVA analysis were used in the RMLMM analysis.

2.2.4. Overstory trees importance value calculations

Importance values (IV) were calculated for all overstory tree species in the study. However, in continuing with the trends above in 2.2., IV are only reported for those species identified in at least three plots. For the remaining species not identified in at least three plots, these species were combined and analyzed as infrequent species.

To investigate shifts in overstory tree IV over time, 1994 was compared to 2017. Importance values were calculated as a sum (300 maximum) of relative density (density of a given species / sum of the densities of all species × 100), relative frequency (frequency of a given species / sum of the frequencies of all species × 100), and relative BA per hectare (BA per hectare of a given species / sum of BA per hectare of all species × 100) as described in (Kent, 2012).

Importance values help to rank species based on their dominance at a site (Kent, 2012), and this value incorporates the number of individuals, its frequency, and its spatial dominance (i.e., BA per hectare) across a defined area (Kent, 2012), making them a valuable tool to describe (and compare) spatial and temporal shifts in overstory tree composition. Importance values can also be helpful in predicting how aggregates of species will change along disturbance gradients or management regimes (Kremen, 2005). In forest research, IV are commonly ranked to show the relative importance of each species at a site. While some researchers report IV as a sum of the three equations above in 2.2.4 divided by three (Plocher, 1999), IV reported here are a true sum of the three percentages (each 100 maximum).

2.2.5. Understory saplings and woody seedlings calculations

For all understory saplings and woody seedlings, abundance and distribution calculations were conducted in JMP® 14 (Cary, NC) to summarize the data by plot, by sample year, and by species. Abundance and distribution summaries were conducted only for the same species identified in our overstory tree analyses, while all remaining species were combined and analyzed as infrequent species.

Further statistical analyses of understory sapling and woody seedling data could not be conducted due to numerous detectable inconsistencies on both the raw field data sheets and in the Microsoft Access database maintained by GRSM. Inconsistencies were attributed to the quality of data collection, rapidly changing climatic conditions, and/or changes in personnel over the 23-year study period.

3. Results

3.1. Overstory trees

3.1.1. Total abundance

A total of 923 live, overstory trees (i.e., tagged trees greater than 3.5 cm DBH) were sampled between 1994 and 2017 across all 10, long-term BBD monitoring plots in GRSM (Fig. 2a). The trees belonged to 20 total species, summarized in Table 2. The number of live, overstory trees sampled varies by plot, by sample year, and by species (Fig. 3a, b, c).

3.1.2. Abundance by plot

Overstory tree abundance (by plot) ranged from 49 to 142 trees (Fig. 2a). Of the 923 total trees, Deep Creek represented the least number of individuals ($n = 49$), and Indian Gap represented the most ($n = 142$; Fig. 2a). All remaining plots fell within these lower and upper limits.

3.1.3. Abundance by sample year

Overstory tree abundance (by sample year) ranged from 429 to 683 trees (Fig. 2b). Of the 923 total trees, 1998 represented the least number of individuals ($n = 429$), and 2010 represented the most ($n = 683$; Fig. 2b). All remaining sample years fell within these lower and upper limits. Over the 23-year study period, the number of live, overstory trees increased from 472 (1994) to 607 individuals (2017);

Table 2
Overstory tree, understory sapling, and woody seedling species observed across 10 long-term high elevation beech forest monitoring plots over the 23-year study period (1994–2017).

Scientific name	Common name	Overstory trees	Understory saplings	Woody seedlings
<i>Abies fraseri</i> (Pursh) Poir ^{1,2,3}	Fraser Fir	✓	✓	✓
<i>Acer pennsylvanicum</i> L.	Striped Maple	✓	✓	✓
<i>Acer rubrum</i> L.	Red Maple	✓	✓	✓
<i>Acer saccharum</i> Marsh.	Sugar Maple	✓	✓	✓
<i>Acer spicatum</i> Lam.	Mountain Maple	✓	✓	✓
<i>Acer species</i> ³	Maple sp.	✓	✓	✓
<i>Aesculus flava</i> Aiton	Yellow buckeye	✓	✓	✓
<i>Amelanchier laevis</i> Wiegand ^{1,2}	Allegheny serviceberry	✓	✓	✓
<i>Amelanchier species</i> ^{1,2}	Serviceberry sp.	✓	✓	✓
<i>Betula allegheniensis</i> Britton	Yellow birch	✓	✓	✓
<i>Betula lenta</i> L.	Sweet birch	✓	✓	✓
<i>Betula species</i> ³	Birch sp.	✓	✓	✓
<i>Fagus grandifolia</i> Ehrh.	American beech	✓	✓	✓
<i>Halesia tetraptera</i> Ellis	Carolina silverbell	✓	✓	✓
<i>Ilex montana</i> Torr. and A. Gray ^{1,2,3}	Mountain winterberry	✓	✓	✓
<i>Magnolia fraseri</i> Walter ^{1,2,3}	Fraser magnolia	✓	✓	✓
<i>Picea rubens</i> Sarg.	Red spruce	✓	✓	✓
<i>Prunus pensylvanica</i> L. ^{2,3}	Fire cherry	✓	✓	✓
<i>Prunus serotina</i> Ehrh. ^{1,3}	Black cherry	✓	✓	✓
<i>Quercus rubra</i> L. ^{1,3}	Red oak		✓	✓
<i>Rhododendron catawbiense</i> Michx. ^{1,3}	Rhododendron		✓	✓
<i>Ribes species</i> ²	Currant		✓	✓
<i>Sorbus americana</i> Marsh. ^{2,3}	American mountain ash		✓	✓
<i>Tsuga canadensis</i> L. ^{1,2}	Eastern hemlock		✓	✓
<i>Viburnum alnifolium</i> Marsh. ^{1,2,3}	Hobblebush		✓	✓

¹ Overstory tree species not identified in at least three plots. These species ($n = 10$) were combined and analyzed as infrequent species.

² Understory sapling species not identified in at least three plots. These species ($n = 10$) were combined and analyzed as infrequent species.

³ Woody seedling species not identified in at least three plots. These species ($n = 11$) were combined and analyzed as infrequent species.

Table 3; Fig. 2b).

3.1.4. Abundance by species

Overstory tree abundance (by species) ranged from 7 to 650 trees (Fig. 2c). Of the 923 total trees, *A. rubrum* represented the least number of individuals ($n = 7$), and *F. grandifolia* represented the most ($n = 650$; Fig. 2c). While 20 total species were identified, only 10 of these species were found in three or more plots (Table 2) and are summarized in Fig. 2c. Eight of these 10 species (*A. pennsylvanicum*, *Acer saccharum* Marsh., *A. spicatum*, *B. allegheniensis*, *B. lenta*, *F. grandifolia*, *Halesia tetraptera* Ellis, and *P. rubens*) increased in abundance, and two (*A. rubrum* and *Aesculus flava*) showed no change in abundance over the 23-year study period (Table 3). The remaining 10 species combined and analyzed as infrequent species decreased in abundance over the 23-year study period (Table 3).

3.1.5. Shifts in community composition

Results from the PERMANOVA analysis showed significant effects of time ($p = 0.001$), plot ($p = 0.001$), and their interaction ($p = 0.001$; Table 4) on community composition. These results are visualized by NMDS in Fig. 3, in which time is represented by contours and communities are represented by ellipses (1 standard error; SE). Early in the time series, communities were more characterized by *F. grandifolia* and *Aesculus flava* with plot specific differences appearing among communities (Fig. 3). Community composition changed (i.e., ellipses elongation and widening due to changes in species' relative BA per hectare)

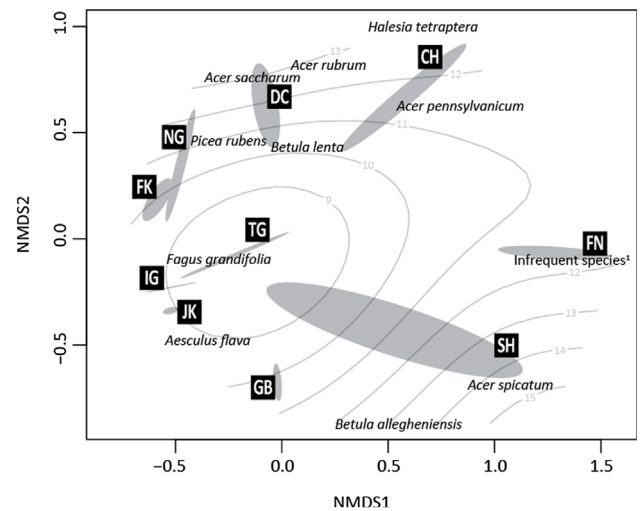


Fig. 3. Non-metric multidimensional scaling (NMDS) visualization of PERMANOVA community analysis for overstory trees over the 23-year study period (1994–2017). The NMDS (2-D stress = 0.14) is based on species' relative basal area for all overstory tree species identified in three or more plots ($n = 10$; see Table 2). Species not identified in at least three plots were combined and analyzed as infrequent species ($n = 10$; Table 2). Gray ellipses (1 SE) represent the 10 plots across all surveys; adjacent black squares indicate plot name abbreviations as in Table 1. Time is represented by contours in the NMDS. Species' positions indicate their influence on composition in the multivariate space, where sites closer to particular species have greater representation by those species.

over time for most plots—following trajectories that are becoming more influenced by *Acer*- and *Betula*-species, with further influences from co-occurring species within plots (Fig. 3).

Each of the 10 plots experienced varying levels of change in community composition over the 23-year study period. Sweat Heifer displayed the greatest amount of community change while Indian Gap, Jenkins Knob, and Gregory Bald experienced the least amount of community change (Fig. 3). Sweat Heifer and Forney Ridge were characterized by *F. grandifolia* early in the time series, while late in the time series these two plots followed trajectories becoming more influenced by *B. allegheniensis*, *A. spicatum*, and members of the infrequent species group (Fig. 3).

Chimneys and Deep Creek followed trajectories that also became less characterized by *F. grandifolia* late in the time series, but instead became more influenced by *A. saccharum* and *Halesia tetraptera* (Fig. 3). Fork Ridge and Newfoundland Gap both became less characterized by *F. grandifolia* late in the time series, but plot specific differences appeared. Fork Ridge experienced the greatest influence late in the time series by *A. saccharum*, while Newfoundland Gap became more influenced by *A. rubrum*, *A. saccharum*, *B. lenta*, *B. allegheniensis*, and *P. rubens* (Fig. 3). Trillium Gap became less characterized by *F. grandifolia* over the 23-year study period, though the influence of *F. grandifolia* still exceeded that of all co-occurring species (Fig. 3). The three plots that experienced the least amount of change in community composition over the 23-year study period (i.e., Jenkins Knob, Indian Gap, and Gregory Bald) are still nearly as heavily characterized by *F. grandifolia* as they were early in the time series (Fig. 3).

3.1.6. Species-specific shifts in basal area

Mean BA per hectare calculations for each of the 10 species identified in three or more plots, plus those combined and analyzed as infrequent species are reported in Table 3 and Fig. 4. Two species (*Aesculus flava* and *F. grandifolia*) showed significant decreases in mean BA per hectare over the 23-year study period, with the greatest decreases in *F. grandifolia* ($-10.33 \text{ m}^2 \text{ ha}^{-1}$; $p < 0.001$) followed by *Aesculus flava* ($-5.51 \text{ m}^2 \text{ ha}^{-1}$; $p = 0.031$; Table 3; Fig. 4).

Table 3

Change in overstorey tree abundance and mean BA per hectare observed across 10 long-term high elevation beech forest monitoring plots over the 23-year study period (1994–2017).

Species	Number of Individuals		Mean BA per hectare ¹		Δ	p-value ²	Directional change in BA ²
	1994	2017	1994	2017			
<i>Acer pennsylvanicum</i> L.	1	8	0.01 (0.01)	0.64 (0.31)	0.63	$p < 0.001$	▲
<i>Acer rubrum</i> L.	5	5	0.24 (0.07)	1.55 (0.37)	1.31	$p < 0.001$	▲
<i>Acer saccharum</i> Marsh.	20	38	1.44 (0.59)	4.38 (1.56)	2.94	$p < 0.001$	▲
<i>Acer spicatum</i> Lam. ³	14	21	0.59 (0.59)	0.88 (0.65)	0.30	$p = 0.260$	NS
<i>Aesculus flava</i> Aiton	22	22	6.98 (3.22)	1.47 (0.90)	- 5.51	$p = 0.031$	▼
<i>Betula allegheniensis</i> Britton	17	28	2.77 (2.44)	5.28 (3.12)	2.51	$p = 0.001$	▲
<i>Betula lenta</i> L.	0	8	0.00 (0.00)	0.64 (0.22)	0.64	$p < 0.001$	▲
<i>Fagus grandifolia</i> Ehrh.	329	411	19.57 (2.91)	9.24 (1.94)	- 10.33	$p < 0.001$	▼
<i>Halesia tetraptera</i> Ellis	5	10	4.01 (2.66)	7.37 (4.20)	3.36	$p = 0.015$	▲
<i>Picea rubens</i> Sarg.	16	24	1.03 (0.54)	4.54 (1.78)	3.51	$p < 0.001$	▲
Infrequent species ⁴	43	32	3.76 (1.67)	5.02 (2.14)	1.26	$p = 0.160$	NS
Total BA ⁵	472	607	30.83 (2.98)	25.42 (2.32)	- 5.41	$p = 0.117$	NS

¹ Mean BA per hectare is followed by SE in parentheses.

² Results from RMLMMs for each species as a function of time. p value is for slopes and the level of significance was set at 0.05. Triangles indicate directional change in mean BA per hectare. Upward facing triangles (▲) indicate significant increases in BA, downward-facing (▼) triangles indicate significant decreases in BA, and 'NS' indicates no significant change in BA.

³ An inaccurate DBH measurement for a single *Acer spicatum* tree appeared in the Sweat Heifer plot in 2006 and was removed prior to RMLMM analysis for that species.

⁴ Infrequent species include analysis of all combined overstorey tree species not identified in at least three plots ($n = 10$; see Table 2).

⁵ Total BA is analysis of the cumulative basal area for all species identified within each plot, plus the infrequent species.

Table 4

Permutational multivariate analysis of variance (PERMANOVA¹) results for community analysis.

	df	F.ratio	R ²	p-value
Time	1	71.856	0.02817	0.001
Plot	9	244.073	0.86114	0.001
Time \times plot	9	21.817	0.07698	0.001
Residuals	86	-	0.03371	-
Totals	105	-	1.00000	-

¹ PERMANOVA includes the analysis of a single matrix, consisting of 106 communities \times 11 species. Of the 11 species analyzed, one includes the combination of 10 species combined and analyzed as infrequent species (Table 2).

Seven species (*A. pennsylvanicum*, *A. rubrum*, *A. saccharum*, *B. allegheniensis*, *B. lenta*, *H. tetraptera*, and *P. rubens*) showed significant increases in mean BA per hectare over the 23-year study period, with the greatest increases in *P. rubens* (+3.51 m² ha⁻¹; $p < 0.001$), followed by *H. tetraptera* (+3.36 m² ha⁻¹; $p = 0.015$), *A. saccharum* (+2.94 m² ha⁻¹; $p < 0.001$), *B. allegheniensis* (+2.51 m² ha⁻¹; $p = 0.001$), and *A. rubrum* (+1.31 m² ha⁻¹; $p < 0.001$; Table 3; Fig. 4). Smaller, but significant increases in mean BA per hectare were also identified in *A. pennsylvanicum* (+0.63 m² ha⁻¹; $p < 0.001$) and *B. lenta* (+0.64 m² ha⁻¹; $p < 0.001$; Table 3; Fig. 4).

No significant change in mean BA per hectare were identified for the 10 species combined and analyzed as infrequent species (+1.26 m² ha⁻¹; $p = 0.160$) and *A. spicatum* (+0.30 m² ha⁻¹; $p = 0.260$; Table 3; Fig. 4). Lastly, analysis of total BA per hectare (all 20 species combined) indicated no significant change (-5.41 m² ha⁻¹; $p = 0.117$) over the 23-year study period (Table 3; Fig. 4).

3.1.7. Shifts in importance

Of the 10 species identified in three or more plots (Table 2), *F. grandifolia* and *Aesculus flava* decreased in importance over the 23-year study period. *Fagus grandifolia* displayed the greatest reduction in IV, followed by *Aesculus flava*—both driven primarily by significant losses in relative BA per hectare (Table 5; Fig. 4). The remaining eight species (*A. pennsylvanicum*, *A. rubrum*, *A. saccharum*, *A. spicatum*, *B. allegheniensis*, *B. lenta*, *H. tetraptera*, and *P. rubens*) became more important over time, with the greatest increases in *A. saccharum*, *B. allegheniensis*, *B. lenta*, *A. pennsylvanicum*, *P. rubens*, and *H. tetraptera*, followed by

minor increases in *A. spicatum*, and *A. rubrum* (Table 5). The remaining 10 species combined and analyzed as infrequent species showed an inconsequential reduction in importance over the 23-year study period (Table 5).

Increases in IV for *A. saccharum*, *B. allegheniensis*, *H. tetraptera*, and *P. rubens* were driven primarily by significant increases in relative BA per hectare over time (Table 5), while *B. lenta* and *A. pennsylvanicum* were driven by sharp increases in relative density, relative frequency, and relative BA per hectare over time—in particular, *B. lenta*, which did not appear in the plots until 2008.

3.2. Understorey saplings and woody seedlings

Due to numerous, detectable data entry inconsistencies on both the raw field data sheets and in the Microsoft Access database maintained by GRSM, understorey sapling and woody seedling data could not be statistically analyzed, beyond abundance and distribution summaries. A common fault identified in the understorey sapling and woody seedling data was due to faulty sampling in the incorrect subplot (and/or subsequently, the incorrect 2 m \times 8 m strip layout) during data collection intervals.

3.2.1. Total abundance

A total of 2,392 live, understorey saplings (i.e., trees exceeding 1.37 m in height (but less than 3.5 cm DBH), were sampled between 1994 and 2017 across all 10, long-term BBD monitoring plots in GRSM (Fig. 5a). The trees belonged to 20 total species, summarized in Table 2. The total number of live, understorey saplings sampled varies by plot, by sample year, and by species (Fig. 6a, b, c).

A total of 584 live, woody seedlings (i.e., woody seedlings tallied and assigned to one of five size class categories) were sampled between 1994 and 2017 across all 10, long-term BBD monitoring plots in GRSM (Fig. 6a). The trees belonged to 21 total species, summarized in Table 2. The total number of live, woody seedlings sampled varies by plot, by sample year, and by species (Fig. 6a, b, c).

3.2.2. Abundance by plot

Understorey sapling abundance (by plot) ranged from 75 to 519 saplings (Fig. 5a). Of the 2,392 total saplings, Deep Creek represented the least number of individuals ($n = 75$), and Fork Ridge represented the most ($n = 519$; Fig. 5a). All remaining plots fell within these lower

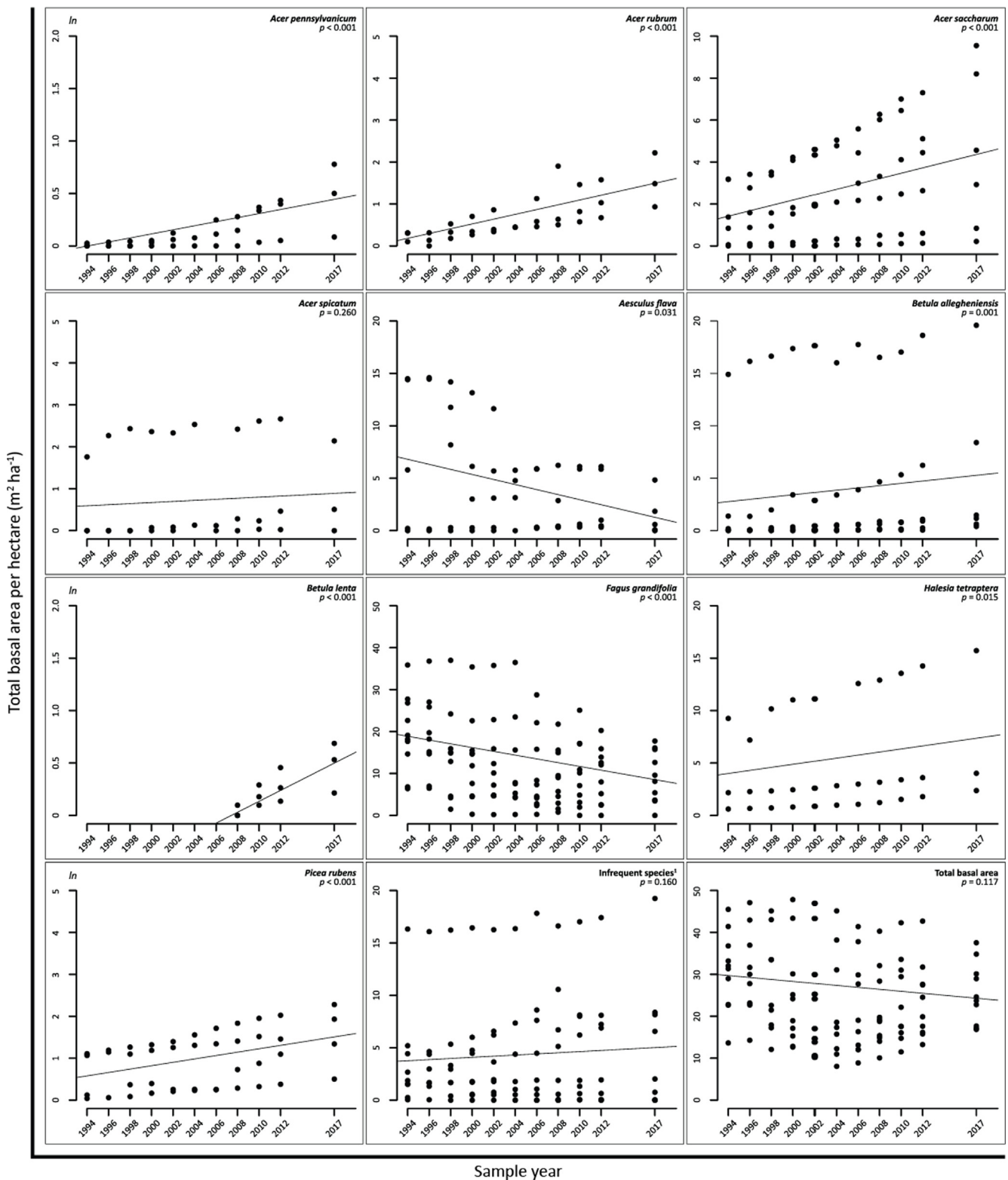


Fig. 4. Overstory tree species-level analysis of basal area per hectare over the 23-year study period (1994–2017). Repeated-measures linear mixed effects models (RMLMMs) were conducted for the 10 species identified in three or more plots ($n = 10$; see Table 2), infrequent species not identified in at least three plots ($n = 10$; see Table 2), and total basal area which includes analysis of all 20 species combined. Note that data were ln-transformed (plus 1) for *Acer pennsylvanicum*, *Betula lenta*, and *Picea rubens* and scale of Y-axis varies by species.

and upper limits. Woody seedling abundance (by plot) ranged from 9 to 127 seedlings (Fig. 6a). Of the 584 total seedlings, Forney Ridge represented the least number of individuals ($n = 9$), and Sweat Heifer represented the most ($n = 127$; Fig. 6a). All remaining plots fell within

these lower and upper limits.

3.2.3. Abundance by sample year

Understory sapling abundance (by sample year) ranged from 98 to

Table 5
Change in overstory tree importance values (IV)¹ observed across 10 long-term high elevation beech forest monitoring plots over the 23-year study period (1994–2017).

Species	Relative frequency		Relative density		Relative BA per hectare		Combined importance values ²	
	1994	2017	1994	2017	1994	2017	1994	2017
<i>Acer pennsylvanicum</i>	2.13	5.56	0.21	1.32	0.01	0.75	2.35	7.63
<i>Acer rubrum</i>	6.38	5.56	1.06	0.82	0.23	1.82	7.67	8.20
<i>Acer saccharum</i>	10.64	11.11	4.24	6.26	2.80	10.34	17.68	27.71
<i>Acer spicatum</i> ³	2.13	3.70	2.97	3.46	0.57	1.04	5.66	8.20
<i>Aesculus flava</i>	8.51	7.41	4.66	3.62	11.32	2.89	24.49	13.92
<i>Betula allegheniensis</i>	10.64	11.11	3.60	4.61	5.39	12.46	19.63	28.18
<i>Betula lenta</i>	0.00	5.56	0.00	1.32	0.00	0.76	0.00	7.63
<i>Fagus grandifolia</i>	21.28	16.67	69.70	67.71	63.47	36.34	154.45	120.71
<i>Halesia tetraptera</i>	6.38	5.56	1.06	1.65	3.90	8.70	11.35	15.90
<i>Picea rubens</i>	8.51	7.41	3.39	3.95	1.33	7.14	13.23	18.50
Infrequent species ⁴	23.40	20.37	9.11	5.27	10.98	17.76	43.49	43.40

¹ IV incorporate relative frequency, relative density, and relative BA per hectare.
² Combined importance values are reported as a sum of the three IV categories (300 maximum).
³ An inaccurate DBH measurement for a single *Acer spicatum* tree appeared in the Sweat Heifer plot in 2006 and was removed prior to IV calculations for that species.
⁴ Infrequent species include analysis of all combined species not identified in at least three plots (n = 10; see Table 2).

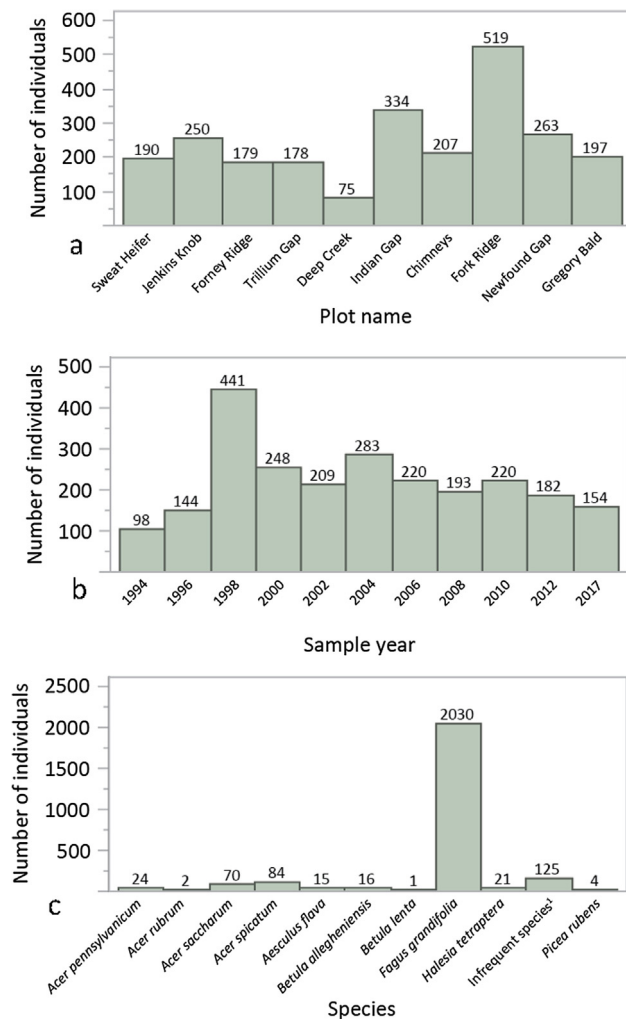


Fig. 5. Abundance and distribution of live, understory saplings observed (n = 2,392) across 10 long-term high elevation beech forest monitoring plots over the 23-year study period (1994–2017). Data organized by plot name (a), by sample year (b), and by species (c). Note y-axis scales vary across Fig. 6a, 6b, and 6c. ¹ Infrequent species includes the 10 understory species not identified in at least three plots (see Table 2).

441 saplings (Fig. 5b). Of the 2,392 total saplings, 1994 represented the least number of individuals (n = 98), and 1998 represented the most (n = 441; Fig. 5b). All remaining sample years fell within these lower and upper limits. Woody seedling abundance (by sample year) ranged from zero to 108 seedlings (Fig. 6b). Of the 584 total seedlings, 1994 represented the least number of individuals (n = 0), and 1996 represented the most (n = 108; Fig. 6b). All remaining sample years fell within these lower and upper limits.

3.2.4. Abundance by species

Understory sapling abundance (by species) ranged from one to 2030 saplings (Fig. 5c). Of the 2,392 total saplings, *B. lenta* represented the least number of individuals (n = 1), and *F. grandifolia* represented the most (n = 2030; Fig. 5c). While 20 total species were identified (Table 2), data are only reported for the same 10 overstory tree species found in three or more plots (Table 2), plus the remaining 10 species combined and analyzed as infrequent species, summarized in Fig. 5c.

Woody seedling abundance (by species) ranged from zero to 375 seedlings (Fig. 6c). Of the 584 total seedlings, *Aesculus flava* and *B. lenta* represented the least number of individuals (n = 0 for both), and *F. grandifolia* represented the most (n = 375; Fig. 6c). While 21 total species were identified, data are only reported for the same 10 overstory tree species found in three or more plots (Table 2), plus the 11 species combined and analyzed as infrequent species, which are summarized in Fig. 6c.

4. Discussion

In high elevation beech forests of Great Smoky Mountains National Park (GRSM), the death of mature, overstory *Fagus grandifolia* trees has contributed to spatial and temporal shifts in forest structure and composition over the past 23 years. While beech bark disease (BBD) has been a well-documented cause of such shifts throughout the north-eastern United States and Europe for over a century (Cale et al., 2017), the degree to which BBD has impacted GRSM high elevation beech forests is less clear as it is difficult to know when the disease complex arrived in different parts of the Park (Ward, 1986). Regardless of the species lost, if a substantial proportion of large, overstory trees is removed from a forest, large-scale changes in forest structure, forest composition, and overall system function can be expected, resulting in a forest stand that is vastly different than its pre-disturbance state (McNulty and Masters, 2005).

GRSM currently represents a disjunct occurrence of the BBD complex and shifts in forest structure and composition have clearly

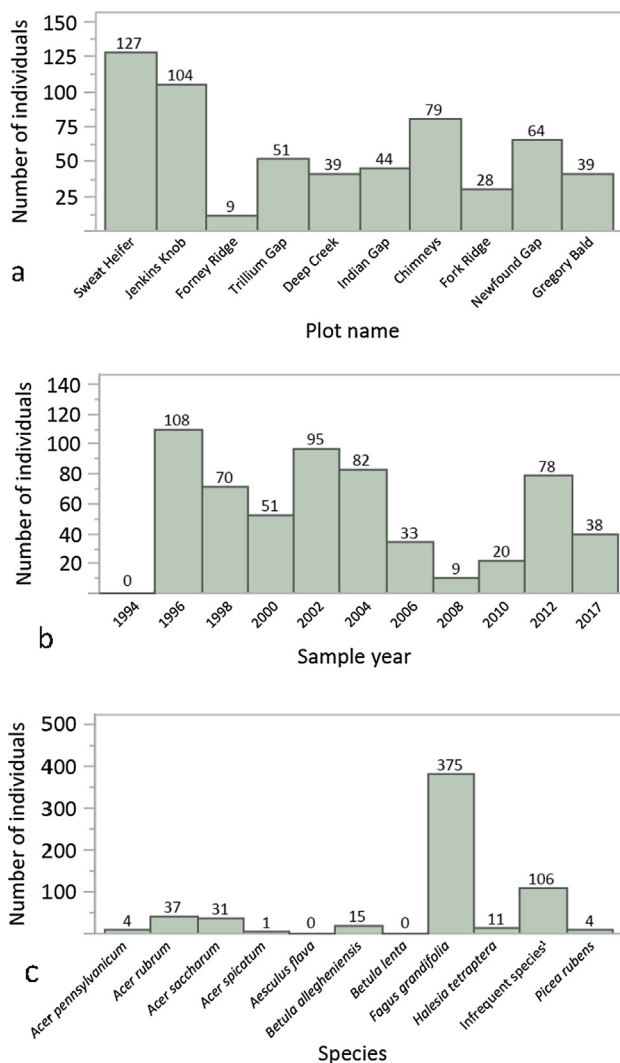


Fig. 6. Abundance and distribution of live, woody seedlings observed ($n = 584$) across 10 long-term high elevation beech forest monitoring plots over the 23-year study period (1994–2017). Data organized by plot name (a), by sample year (b), and by species (c). Note y-axis scales vary across Fig. 6a, b, and c. ¹ Infrequent species includes the 11 understory species not identified in at least three plots (see Table 2).

occurred there. Beech bark disease is now well established in the Park and continues to threaten *F. grandifolia* trees within high elevation beech forest habitats. While not quantified, visual evidence of both the scale insect and the fungus was noted in nine of the 10 plots sampled. The only plot lacking this evidence was Sweat Heifer, a plot that experienced the complete extirpation of overstory *F. grandifolia* trees by 2010. Regardless of scale density as rated in 1994 (Table 1), the arrival of BBD (and resulting decrease in *F. grandifolia* basal area; BA) has spread relatively quickly throughout the Park.

Stratified dispersal of *Cryptococcus fagisuga* (i.e., the formation of isolated colonies ahead of the advancing front) is most likely occurring in GRSM, expediting the spread of BBD throughout the Park. While *C. fagisuga* has only invaded ~27% of the geographical range of *F. grandifolia* as of 2005 (Morin et al., 2005; Cale et al., 2017), BBD is expected to continue its range expansion, particularly in regions where the host tree is a dominant component in forest stands (Morin et al., 2007)—such as in GRSM high elevation beech forests. As densities of *C. fagisuga* increase, the odds of later infection by the exotic fungus (*Neonectria faginata*) also increase, further expediting the death of mature *F. grandifolia* trees (Cale et al., 2015).

The BBD complex was first confirmed in GRSM at the intersection of the Appalachian trail and the Sweat Heifer trail near the center of the Park (Ward, 1986), yet the greatest losses in BA began in more northerly plots, and generally travelled towards the southwest edge of the Park (i.e., Trillium Gap, Newfound Gap, Sweat Heifer, Chimneys, Indian Gap, Fork Ridge, Jenkins Knob, Fork Ridge, Deep Creek, and lastly, Gregory Bald; Fig. 1). Based on the inferred stage of the BBD outbreak (and the subsequent reductions in *F. grandifolia* BA within each plot), it appears that the spread of BBD throughout the Park has not been consistently unidirectional.

Our current understanding suggests that BBD was first noted near the center of the Park and subsequently spread outward from there. Particularly relevant to our study, the spread appears to have occurred more rapidly in an eastward direction. This seems consistent with the density of high elevation beech forests more typically described as beech gaps or beech orchards, which is greatest in the eastern part of the Park. In absence of additional long-term monitoring plots in this region, it limits our ability to depict the full story of BBD in the Park. The timing of arrival, severity of impact, and stage of recovery of individual plots are clearly different, suggesting a potentially complex history in this system. Adding plots to monitor future responses to repeated outbreaks could further clarify these patterns.

As a foundational species in GRSM high elevation beech forests, *F. grandifolia* is an autogenic ecosystem engineer, meaning one that directly or indirectly modulates the availability of resources to other species (Jones et al., 1994). In doing this, autogenic engineers create, maintain, and modify their habitats through their physical structures (and in forest stands, this occurs through both living and dead tissues; Jones et al., 1994). The role *F. grandifolia* plays within these high elevation beech forests is not likely one to be easily assumed by another species due to *F. grandifolia* being one of the primary hard-mast tree species found throughout the high-elevation northern hardwood forests of the Southern Appalachian Mountains (Eiler et al., 1989).

The data from this study support the hypothesis that the death of mature, overstory *F. grandifolia* trees within GRSM high elevation beech forests has contributed significantly to spatial and temporal shifts in forest structure and composition over the past 23-years. The implementation of the long-term, BBD Monitoring Protocol in 1994, has helped to capture what effects BBD has had on overstory *F. grandifolia* trees (and its co-occurring species) within a unique, critically-imperiled forest community, GRSM high elevation beech forests.

4.1. Direct impacts from the loss of overstory *Fagus grandifolia*

In GRSM, the number of mature (i.e., greater than 3.5 cm diameter breast height; DBH), overstory *F. grandifolia* trees has been significantly reduced over the past 23-years. Since 1994, mean BA per hectare for the species has declined by 53%, yet, the number of individuals has increased by 25% (Table 3). The sharpest declines in both abundance and BA per hectare occurred between 1994 and 2004. These sharp declines are most likely indicative of the killing front as described by Shigo (1972).

Following the killing front, by 2006, beech abundance began increasing (peaking in 2010). Mean basal area appears to have reached some stabilization at ~9 m² per hectare between 2006 and 2017. This is indicative of the aftermath stage as described by Shigo (1972), whereby *F. grandifolia* trees can be found in various stages of decline. In GRSM, the trends following the aftermath stage appear to closely resemble those seen in the northeast, where host tree populations decline, and beech thicket formation (via root sprouting or seed origin) increases (Giencke et al., 2014). The addition of numerous, smaller individuals into these GRSM plots indicates that beech thicket formation is most likely occurring (possibly due to root sprouting (Morris et al., 2014)). However, it could also be the case that these new canopy gaps have promoted the influx of individuals from seed origin as noted by (Giencke et al., 2014), though the present study does not attempt to

answer the question of source of new *F. grandifolia* recruitment. To clarify which of these reproductive mechanisms is driving thicket formation in GRSM, further molecular analyses would likely be required.

While both *F. grandifolia* and *Aesculus flava* have seen drastic reductions in mean BA per hectare since 1994, all remaining species analyzed in this study increased significantly over time (except for *Acer spicatum*; Table 3). The resulting increase in mean BA per hectare for these co-occurring species led to a non-significant decline ($p = 0.117$) in total BA per hectare (for all 20 species combined) over the 23-year study period (Table 3). This demonstrates that *F. grandifolia* and *Aesculus flava* are already being replaced by co-occurring species within the plots, with the greatest influences coming from the four *Acer* species, the two *Betula* species, *Halesia tetraptera*, and *Picea rubens* (Table 3). While most of these species have been present in the plots since 1994 (except *Betula lenta*, which did not appear until 2008; Fig. 4), new canopy gaps created by the death of *F. grandifolia* and *Aesculus flava*, have allowed these co-occurring species to gain increased dominance, either in the number of individuals, or in mean BA per hectare, or both (Table 3). In an old-growth forest in northeastern Ohio, Forrester and Runkle (2000) found the importance of *F. grandifolia* decreased over time while *Acer saccharum* increased in importance, a trend also seen in the GRSM long-term BBD monitoring plots. The replacement of hardwood species by *Acer* species is a common theme across the United States and is cause for concern for the fauna that rely on the consumption of beech nuts and acorns (Gillen and Hellgren, 2013).

Historically, BBD was expected to most easily spread into areas of increasing beech density. However, Morin et al. (2007) found that rates of BBD spread were more influenced by dispersal of *C. fagisuga* than by *F. grandifolia* stem density. Since GRSM high elevation beech forests are dominated by *F. grandifolia*, the stratified dispersal of *C. fagisuga* (and subsequent fungal infections) is clearly showing the capacity to drive notable changes within these critically imperiled, G1-ranked forest communities, potentially pushing them closer to extinction (NatureServe, 2018). As *C. fagisuga* populations now have a wide distribution throughout GRSM, BBD is likely to remain as a long-term forest pest as has been seen in the northeast (Cale et al., 2017).

4.2. Overstory tree species shifts in importance

Mimicking trends identified in overstory tree BA reductions, both *F. grandifolia* and *Aesculus flava* have become less important overstory (i.e., decreased Importance Values, IV) forest components in GRSM high elevation beech forests, while all remaining co-occurring species have become more important over the 23-year study period (Table 5). The increases in IV for these co-occurring species are being driven primarily by increases in their relative BA per hectare, rather than their relative frequency or relative density. These primary increases in relative BA are indicative of the co-occurring species simply growing larger in size, rather than them recruiting new individuals into the plots. This can be described as slow dynamics, in which insect- and disease mediated disturbances lead to gap recruitment that is different than what would occur in most temperate forests from the creation of a single canopy gap (McCarthy, 2001).

In slow dynamics, trees that die (but remain standing) will affect resource release and allocation differently (to those co-occurring species) than would the loss of a single, mature individual after its immediate removal from the system (McCarthy, 2001). Recalling that GRSM high elevation beech forests reside in a northern hardwood forest type and border the Park's boreal spruce-fir matrix, a greater appreciation of these regional dynamics should be considered, particularly when discussing a critically-imperiled forest community like high elevation beech forests.

While reduced to smaller stemmed, stunted individuals by 2017, *F. grandifolia* remains as the most important overstory tree species in GRSM high elevation beech forests, showing IV more than 4x that of the next two closest species, *Betula allegheniensis* and *A. saccharum*

(Table 5). *Betula allegheniensis* has a wide distribution across many community types in GRSM, with the highest population densities occurring ~914 m, and a second, higher-elevation group forming in the spruce-fir matrix ~1372 m (Whittaker, 1956). Over the 23-year study period, *B. allegheniensis* has become more important in GRSM high elevation beech forests (Table 5), benefiting from the significant decreases in *F. grandifolia* and *Aesculus flava* BA. As an important component of northern hardwood forests, *B. allegheniensis* is likely to remain as a long-term, equally-important species in the gray beech forests of GRSM (Whittaker, 1956).

Acer saccharum is also frequent and widely distributed throughout the Park. Of the four *Acer* species analyzed, *A. saccharum* experienced the greatest increases in IV over time, a theme concurrent in the northeast, particularly in the Adirondack Mountains. Species dominants that persist following BBD in this northern hardwood forest type include *A. saccharum*, *F. grandifolia*, and *B. allegheniensis* (Giencke et al., 2014), three species that remain as the most important overstory tree species in GRSM high elevation beech forests as of 2017 (Table 5). In northern hardwood forests long-afflicted by BBD, comparisons of the two systems (even though spatially distant from one another) become a viable option, as we see similar effects of root sprouting now being produced in GRSM high elevation beech forests. Therefore, the re-infection of aftermath forests in GRSM remains as a threat, potentially leaving BBD as a long-term forest component in the Park.

4.3. Understory sapling and woody seedling responses

While reciprocal replacement of *F. grandifolia* and *Aesculus flava* was identified for the overstory tree analyses, it appears that the understory response of GRSM high elevation beech forests are displaying a strong tendency for self-replacement (Forrester and Runkle, 2000), as evidenced by the dominance of *F. grandifolia* stems in both the understory sapling and woody seedling categories (Fig. 6c, c). *Fagus grandifolia* comprises 85% of all understory saplings (2,030 of 2,392 individuals; Fig. 5c), and 64% of all woody seedlings (375 of 584 individuals; Fig. 6c).

As one of the most shade tolerant species in North American forests, *F. grandifolia* grows well beneath a closed canopy (Forrester and Runkle, 2000), and understory saplings of the species appear to be benefiting most from new canopy gaps created by the loss of mature, overstory individuals. Other abundant (i.e., > 20 individuals) understory saplings identified in this study are *Acer pennsylvanicum*, *A. saccharum*, *A. spicatum*, and *H. tetraptera*, with all remaining species showing negligible abundance in the understory (Fig. 5c). Combined understory sapling abundance (all species included) appear to have peaked in 1998, and generally declined through 2017 (Fig. 5b).

With respect to woody seedlings, *Acer rubrum* and *A. saccharum* were the next most abundant species (i.e., > 20 individuals) relative to *F. grandifolia* (Fig. 6c). While multiple *A. rubrum* woody seedlings were identified over the 23-year study period, their survival at these relatively high-elevations in GRSM high elevation beech forests is low. High mortality rates were observed for *A. rubrum* woody seedlings, with only two of the 37 woody seedlings successfully progressing into the understory sapling category (Fig. 5c). Long-term successional patterns identified for woody seedlings in GRSM high elevation beech forests (all species combined) displayed very low success rates with just over 2% (12 of 584 individuals; data not shown) successfully achieving the final size class category (i.e., woody seedlings greater than 1 m tall) and having the ability to progress into the understory sapling category.

4.4. Expected indirect ecological impacts of beech bark disease in Great Smoky Mountains National Park

The invasion of exotic forest pests and pathogens into a system alter the physical properties of that ecosystem (Crooks, 2002). These physical property changes are more commonly researched (Held, 1983;

Jones et al., 1989; Cassagne et al., 2004; Lovett et al., 2010) because they are more easily measured than the more subtle shifts that will ultimately determine the way in which species will respond to those changes (Crooks, 2002). Many lines of research emphasize that BBD has the greatest impact on vegetation structure and mast availability—two critical factors that have the potential to drive subsequent changes in animal behavior (Storer et al. in Evans et al., 2004)

Fagus grandifolia, as an autogenic engineer influences both the physical and biotic properties of GRSM high elevation beech forests. Following the loss of an autogenic engineer, potential negative (and positive) impacts will be seen in the biota that utilize these habitats. These influences include food production (Gillen and Helgren, 2013), maintenance of canopy closure, moisture levels, and light regimes (Storer et al. in Evans et al., 2004), and soil properties (Cassagne et al., 2004). In GRSM, the loss of *F. grandifolia* from high elevation beech forests, as an important hard mast species in high elevations is likely to further impact large mammal populations.

While some lines of evidence have shown that canopy openings (promoted by mature beech mortality) have been filled by understory beech saplings already present in the understory (Giencke et al., 2014), these smaller beech thickets do not always satisfy the requirements for the fauna that once utilized the beech resource, and as a slow-growing species, the effects will be long-lasting. Beech prospers due to its ability to tolerate extreme shade and its ability to reproduce vegetatively via root suckering, allowing it to gradually become dominant at the expense of other tree species (Jones et al., 1989).

5. Conclusion

In GRSM, some high elevation beech forests have been affected by BBD for at least 30 years (Ward, 1986). The BBD Monitoring Protocol sought to identify patterns of infestation, spread, and host mortality at 10 high elevation beech forest plots throughout the Park. While the long-term future of *F. grandifolia* within these 10 plots is yet to be determined, it is most likely that numerous, smaller individuals will most likely have fates like their parents. Ecologically though, the root sprouting nature of *F. grandifolia* could be an advantage for the species. The loss of a few venerable trees, giving rise to numerous juveniles could potentially even support larger wildlife communities in the future, depending on how BBD affects these high elevation beech forests in the aftermath stage (Houston, 1975).

Giencke et al., (2014) showed that understory saplings (in a 5.0 – 9.9 cm [2.0–3.9 in.] DBH class) in the Adirondack Mountains were being re-infected in aftermath forests long impacted by BBD, with remaining *C. fagisuga* populations from mature trees acting as a source of inoculum. This seems to be a pattern that is already culminating in GRSM high elevation beech forests as evidence of *C. fagisuga* was found in all plots sampled in 2017. With the mean DBH of *F. grandifolia* being reduced to just 9.35 cm (3.68 in.) in GRSM high elevation beech forests, a secondary killing front is likely to occur as these individuals mature. While we are only getting a brief snapshot of the species lifespan, the dominance of *F. grandifolia* in the understory is promising, though its potential to obtain its overstory status once again is likely going to be limited and slower progressing.

In these high elevation beech forests, BBD has reduced larger DBH, mature overstory individuals to smaller DBH individuals. The elimination of mature beech from GRSM high elevation beech forests as a result of BBD, supports that the complex is likely to remain as a long-term component of these critically-endangered forest communities as witnessed by the results of this 23-year study. Originally deemed an invaluable species by many foresters throughout the 1950's (Shigo, 1972), we now know the role of *F. grandifolia* extends well beyond that of a species which provides valuable lumber. GRSM high elevation beech forests, being critically imperiled forest communities, contribute to the Park's status as both an International Biosphere Reserve and a World Heritage Site, and therefore, continued research of the BBD

complex in the Park should be considered.

While the effects of BBD are becoming better understood following nearly a century of research, in 2016, a new forest health alert was issued for *F. grandifolia* in Ohio, yet, no causal agent has been identified to date (Pogacnik and Macy, 2016). This new arboreal mystery is known as beech leaf disease (BLD). Symptoms of the disease begin with a dark striping between leaf veins (followed by later chlorotic symptoms), shriveling of leaf clusters, and reduced leaf and bud production (Pogacnik and Macy, 2016). Saplings of the species appear to be increasingly affected by BLD, with rapid declines seen in just a few years, while in larger, overstory trees, BLD seems to progress slower (Pogacnik and Macy, 2016).

In Ohio, where BLD is well established, symptoms appear on nearly 100% of beech trees (Pogacnik and Macy, 2016). With the loss of mature, overstory *F. grandifolia* trees in GRSM, and the abundant response by the understory saplings, the newly-developing BLD could certainly become a candidate to afflict beech trees within the Park, further endangering *F. grandifolia*'s long-term survival and persistence in GRSM high elevation beech forests.

CRediT authorship contribution statement

Lee Rumble: Conceptualization, Investigation, Data curation, Formal analysis, Writing - original draft. **Glenn Taylor:** Conceptualization, Investigation. **Joshua B. Grinath:** Formal analysis, Writing - review & editing. **Ashley B. Morris:** Investigation, Writing - review & editing, Supervision.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.117954>.

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