

**MEASURING SPATIAL AND TEMPORAL SHIFTS
IN BEECH GAP FOREST STRUCTURE AND COMPOSITION
IN RESPONSE TO BEECH BARK DISEASE
IN GREAT SMOKY MOUNTAINS NATIONAL PARK**

by

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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. In Great Smoky Mountains National Park (GRSM), high-elevation beech gaps are dominated by American beech (*Fagus grandifolia* Ehrh.)—a tree species that has been severely impacted by Beech Bark Disease (BBD), a non-native pathogenic complex first confirmed in the Park in 1986. In 1994, a long-term monitoring protocol was established by Park foresters to document patterns of BBD infestation, progression, and host mortality at 10 beech gap plots established throughout GRSM. The analysis of a 23-year dataset supports that the reduction in *F. grandifolia* basal area is driving significant shifts in forest structure and composition. The decline of the foundational species, *F. grandifolia* from high-elevation beech gaps will have broad consequences for associated biota, ecosystem function, and potentially, the long-term persistence of beech gaps in GRSM.

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CHAPTER ONE

BACKGROUND AND OBJECTIVES

Forests, forest disturbances, and forest pests and pathogens

Forests cover approximately 30% of the Earth's land surface (~42 million km²), providing numerous ecological, economic, social, and aesthetic benefits (Bonan, 2008). They are biological hotspots comprised of vast assemblages of plant and animal species, and they heavily influence climatic patterns through various exchanges with the atmosphere (Bonan, 2008). Temperate forests and their distribution throughout North America are the result of past land-use and disturbance histories, whether naturally-or anthropogenically-created (Braun, 1950; Harmon et al., 1984; Dale et al., 2001). Ultimately, these disturbance regimes influence forest composition, forest structure, and ecosystem-level processes (Lovett et al., 2006), extending well beyond the terrestrial landscape, further influencing aquatic resources and overall climatic patterns (Dale et al., 2001; Ellison et al., 2005).

A disturbance is any event in time that disrupts an ecosystem, a community, or population—ultimately altering resources, substrate (and nutrient) availability, or the physical environment (Christensen, 2014). These changes can be the result of biotic or abiotic factors and can include any combination of the two. Drought (Anderegg et al., 2012), fire (Arthur et al., 2015), wind (Nagel and Diaci, 2006), ice (Irland, 2000), deforestation (Gough et al., 2016), resource extraction (Wickham et al., 2007), habitat

fragmentation (Haddad et al., 2015), and exotic forest pests and pathogens (Lovett et al., 2006) all have the potential to alter forest structure and composition over large areas of land. Furthermore, each disturbance type differs in its frequency, extent, and severity (Dale et al., 2001), and ecosystem responses to these disturbances will vary across environmental gradients as a result (Harmon et al., 1984).

Exotic forest pests and pathogens are among the most serious environmental threats to millions of hectares of forested land worldwide (Castello et al., 1995; Karel and Man, 2017), often as a result of human introduction (Cappaert et al., 2005; Ellison et al., 2005; Dodds and Orwig, 2011; Giencke et al., 2014). In 2015 alone, more than 24,000 km² (~2.4 million hectares) of tree mortality were reported by the United States Forest Service (USFS)—with 22% of this mortality coming from a single forest pest, western mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Karel and Man, 2017). As seen with *D. ponderosae*, forest pests have the potential to impact large areas of forested land by colonizing common host trees, such that their influence on a single species across a forest landscape can be widespread and long-lasting (Lovett et al., 2006).

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

In the eastern United States, forests have routinely experienced destructive forest pests and pathogens: chestnut blight (Woods and Shanks, 1957), Dutch elm disease (Castello et al., 1995), hemlock woolly adelgid (Krapfl et al., 2011), dogwood anthracnose (Jenkins and White, 2002), emerald ash borer (Herms and McCullough, 2014), Asian longhorned beetle (Dodds and Orwig, 2011), and beech bark disease (Cale et al., 2017)—all of which have altered forest structure and composition over large 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. Spreading at a historic rate of 14.7 ± 0.9 km/year, this pathogenic complex has targeted American beech (*Fagus grandifolia* Ehrh.), most severely impacting forests containing large proportions of *F. grandifolia* (Morin et al., 2007). Morin et al., (2007) suggested that BBD is likely to continue expanding its range over the next 50 years, though models built

from empirical data do not always accurately predict range expansion rates (Hastings et al., 2005). Particularly problematic is that the scale insect associated with BBD shows patterns of stratified dispersal, along with discontinuous, long-range expansion (Morin et al., 2007). Stratified dispersal is characterized by the formation of isolated colonies ahead of the advancing front, whereby invasions advance from several locations which ultimately coalesce with the rest of the population. This stratified dispersal can expedite spread rates beyond that of those from just a single location (Hastings et al., 2005). This, along with discontinuous, long-range expansion has allowed for the formation of disjunct populations such as has been seen with BBD (Figure 1; Morin et al., 2007).

Beech bark disease

In North America, BBD is a non-native pathogenic complex afflicting *F. grandifolia* 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 (*Xylococcus 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 an introduced European fungus (*Neonectria faginata* (Pers.:Fr.) Fr. Var. Lohman, A. M. Watson, & Ayers) or a native fungus (*Neonectria ditissima* (Tulasne & C. Tulasne) Samuels & Rossman; Wiggins et al., 2004; Cale et al., 2015). Combined, the BBD complex has led to extensive mortality of *F. grandifolia* trees, decreases in net forest primary 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, due to an absence of *Neonectria* species, and is instead recognized by a proliferation of scale populations (Shigo, 1972). The killing front is characterized by extensive tree dieback and aboveground tree mortality. During the killing front, both the scale insect and the fungus can be seen on more than 90% of stems within a single stand (Ehrlich, 1934). In the killing front, infections by *Neonectria* species coalesce and begin girdling trees, with stands showing losses as high as 50% within seven years for trees greater than 20 cm (Miller-Weeks, 1982). Finally, 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 even the complete extirpation of mature trees. Following the aftermath stage, as host tree populations decline, scale populations, *Neonectria* spp. 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). Both the non-native beech scale (*C. fagisuga*) and the introduced European fungus (*N. faginata*) are believed to have made their way into Halifax, Nova Scotia, circa 1890 on stocks of ornamental European beech trees (Wiggins et al., 2004).

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). By 1932, the BBD complex was established (as evidenced by the death of *F. grandifolia* trees) throughout eastern and south-central Maine (Houston, 1975). However, the disease was not initially seen as a detriment to forest health (and was even welcomed by some; Shigo, 1972) as *F. grandifolia* was deemed by foresters at the time to be an invaluable tree species due to its weed-like growth habit (i.e., root sprouting), which shaded out the more profitable hardwood species (Shigo, 1972; Cale et al., 2017). 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, beech forests of Great Smoky Mountains National Park (GRSM; Figure 1; Wiggins et al., 2004; Cale et al., 2017).

The host tree (*Fagus grandifolia*)

Fagus grandifolia is a foundational tree species and major component of forests throughout eastern North America (Cale et al., 2017). The species covers a wide geographic range—extending north into Nova Scotia and south into northern Florida, and westward into southern Ontario, and eastern Texas (Tubbs and Houston, 1990). A limited population of Mexican beech (*F. grandifolia* var. *mexicana* Martínez) can also be found in the Sierra Madre Oriental mountain range in Mexico, though its distribution is restricted to ~10 populations (Williams-Linera et al., 2002). As a temperate, shade tolerant species, *F. grandifolia* can live for 300-400 years, and reproduces both sexually and asexually (Oliver and Larson, 1990; Tubbs and Houston, 1990). In GRSM, tree cores identified by Blozan (1995) found *F. grandifolia* trees within nine of the 10 plots sampled in this study averaged 112 years of age (with a range from 34 to 220 years old). Sexual reproduction in *F. grandifolia* leads to autumnal beechnut masts, with heavy seed production occurring in 2- to 8-year intervals, although significant fruit crops may not appear until trees reach age 40, with the most abundant masts occurring by age 60 (Tubbs and Houston, 1990). These autumnal beechnut masts can lead to periodic pulses of beech tree regeneration via seeds (Cale et al., 2017).

Camp (1950) described three basic types of *F. grandifolia* (based on morphological and ecological criteria)—gray, red, and white beech. Camp (1950) further hypothesized that these types were three unique species prior to Pleistocene glaciation, which ultimately forced these species into contact with one another. In the Southern Appalachian Mountains, gray type are found in high-elevation (above 1,370 m) beech forests, red type are found at mid elevation (762 m – 1,066 m) on well-drained slopes (occurring as more of a continuation of the upper cove mixed-deciduous forests), and white type are found at low elevation (below 762 m). Red and gray types can be challenging to distinguish from one another morphologically, while white types are more easily identified (Cooper and Mercer, 1977).

Whittaker (1956) further describes sharply distinct differences between north- and south-facing gray beech forests, with north-facing gray beech forests appearing more as a continuation of the upper cove mixed deciduous forests; hosting both red and gray types. North-facing gray beech reside in a more mesic forest type that is distinguished by a greater number of stems, small stem diameters, and found interspersed among other subalpine flora (Whittaker, 1956). South-facing gray beech forests are markedly different and are the least frequent type of beech forest identified in the Park (Whittaker, 1956). These south-facing gray beech forests are distinguished by an absent shrub layer, a distinctive herb stratum dominated by sedges (covering up to 90% of the forest floor), and reduced species diversity (Whittaker, 1956).

Older trees (i.e., larger diameter breast height [DBH; measured 1.37 m from ground level on the high side of the slope]; Millers et al., 1992) are more susceptible to BBD (Wiggins et al., 2004). An estimated 1% of trees long-affected by BBD appear to have at least some resistance against *C. fagisuga* (Houston, 1994), with resistant individuals often appearing as clonal clusters formed within a stand (Houston, 1982). Still, the number of trees resistant to *C. fagisuga* in a stand is much lower than the number of susceptible trees, possibly due to the clonal nature of *F. grandifolia* in GRSM (Morris et al., 2004, 2014).

Only a small number of studies have been conducted to understand *F. grandifolia*'s resistance to *C. fagisuga* (Ćalić et al., 2017). Resistance to *C. fagisuga* is thought to be a heritable trait, though little is known about the specific mechanisms behind phenotypic resistance (Koch et al., 2010). Trees with low levels of beech scale may or may not develop BBD. It is also possible that a specific threshold of scale insects are required before *Neonectria* species can become established, or that low levels of *C. fagisuga* infestations on small stems could promote BBD resistance as trees mature (Koch et al., 2010). While molecular markers have been identified that define modes of inheritance, no markers have been identified for individual tree resistance (Ćalić et al., 2017). In a recent publication (Ćalić et al., 2017), a genome-wide association study (GWAS) identified a single locus that contributes to resistance, with four significant SNPs on chromosome 5 showing significant associations for beech scale resistance in a gene coding for a metallothionein-like protein. It is believed these proteins sequester excess

metal ions, and could play a role in resistance to *C. fagisuga*, though replication of the GWAS is needed to confirm the SNPs are truly associated with the scale-resistant trait (Ćalić et al., 2017).

Since *C. fagisuga*, *X. betulae*, and *Neonectria* species use living tissue for feeding, Ehrlich (1934), hypothesized that beech scale insects were a sole and necessary predisposing factor for later infection by *Neonectria* species. This was further supported by Wiggins et al., (2004) who found increasing *F. grandifolia* mortality as populations of *C. fagisuga* increased. Wiggins et al., (2004) also found *X. betulae* to be significantly associated with *F. grandifolia* trees prior to their mortality in GRSM—only decreasing as host tree mortality increased. This supports the relationship dynamics of both the scale insects and the later infection by either *Neonectria* species, which ultimately girdle and kill susceptible trees. By better understanding the genetic architecture of *F. grandifolia*, breeding programs could potentially develop resistant *F. grandifolia* cultivars that could be implemented in forests long-impacted by BBD (Ćalić et al., 2017).

Exotic pests and pathogens in GRSM

GRSM is one of the largest expanses (211,415 ha) of protected forest in the eastern United States (National Park Service, 2011). The Park was established in 1934, resides in both Tennessee and North Carolina, and is part of the Southern Appalachian Mountains—nested within the Blue Ridge physiographic province (United States Geological Survey, 2017). Of the Park's land area, nearly 95% is forested with elevations

ranging from 221 m to 2,025 m (Beeman and Pelton, 1980). This great relief leads to complex ecological gradients, and the Park is internationally renowned for its biological diversity and species richness (Whittaker, 1956; Jenkins, 2007). The Park is both an International Biosphere Reserve and a World Heritage Site due to its biological importance and diverse biological communities (Jenkins, 2007).

Exotic pests and pathogens were present in the Park prior to its establishment. In GRSM, exotic diseases, insects, and plants have been the most destructive biotic factors in the Park, contributing to shifts in forest structure and composition (Jenkins, 2007), often as a result of human introduction (Harmon et al., 1984; Jenkins and White, 2002; Wiggins et al., 2004; Krapfl et al., 2011). Lacking natural predators, exotic pests and pathogens can exert significant dominance on a landscape, leading to species declines and reductions in overall biological diversity. While not all-inclusive, notable forest pests and pathogens responsible for these changes in the Park include: chestnut blight (Woods and Shanks, 1957), balsam woolly adelgid (Taylor, 2012), hemlock woolly adelgid (Krapfl et al., 2011), dogwood anthracnose (Jenkins and White, 2002), emerald ash borer (Taylor, pers. comm., 2017), and BBD (Wiggins et al., 2004).

In the Park, three long-term forest health monitoring programs have been implemented to document changes in forest structure and composition at the landscape level (Taylor, 2012). These monitoring programs have been implemented for: 1) balsam woolly adelgid (*Adelges piceae* Ratzeburg)—a non-native aphid-like insect that feeds on the trunks and limbs of Fraser fir (*Abies fraseri* (Pursh) Poir.) trees (implemented in

1986); 2) butternut canker (*Ophiognomonia clavignenti-juglandacearum* (Nair, Kostichka, & Kuntz) Broaders & Boland)—a non-native fungal disease that forms cankers along the trunks and stems of butternut trees (*Juglans cinerea* L.), thus compromising their structural integrity (implemented in 1987); and 3) BBD as described above (implemented in 1994). Implementation of pest- and disease-monitoring programs within specific forest types allows Park biologists to better understand patterns of infestation and progression, host mortality, and influence on overall forest health. Monitoring programs become particularly crucial for host trees that have restricted habitat requirements and distributions (such as the high-elevation beech forests of GRSM) which are currently threatened by BBD.

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 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 *Beech Bark Disease Monitoring Protocol for Great Smoky Mountains National Park* was established by the National Park Service in 1994 to monitor and

document patterns of infestation, progression, and host mortality in 10 beech forests throughout GRSM (Blozan, 1995; Taylor, 2006).

In GRSM, BBD has been impacting *F. grandifolia* trees for more than 30 years. As seen in the northeast, BBD will likely remain as a long-term part of the Park's forest ecosystem (Cale et al., 2017). While impacting *F. grandifolia* trees in the Park, the indirect effects induced by BBD will further hinge on the forest type in which the species resides, the overall species composition in a stand, and the environmental gradient in which this species resides on the landscape (Harmon et al., 1984; Kupfer and Cairns, 1996). The loss of mature, overstory *F. grandifolia* trees is likely to have significant deleterious effects on stands containing the highest proportions of mature *F. grandifolia* trees (Morin et al., 2007), while further impacting their co-occurring flora and fauna, and overall forest health in the Park.

Beech gaps of GRSM

Great Smoky Mountains National Park has a long history of anthropogenic disturbance (e.g., logging, settlement, and farming) which has ultimately shaped the landscape seen today (Jenkins, 2007). While many disturbance regimens of the past have since disappeared, new impacts still today extend into Park boundaries driving notable changes in forest structure and composition (Tuttle, 2007). Threats now come in the form of climate change (Dale et al., 2001), increased acid deposition (Robinson et

al., 2008), and most notably, exotic forest pests and pathogens (Wiggins et al., 2004; Lovett et al., 2006; Morris et al., 2009; Krapfl et al., 2011; Giencke et al., 2014).

In GRSM, Whittaker (1956) described fifteen climax forest types—from low elevation mixed cove hardwoods of Eastern hemlock (*Tsuga canadensis* L.), American hornbeam (*Carpinus caroliniana* Walter), flowering dogwood (*Cornus florida* L.), yellow poplar (*Liriodendron tulipifera* L.), sweet birch (*Betula lenta* L.), and red maple (*Acer rubrum* L.) to high-elevation boreal forests, where the dominant forest type above 1,370 m is a red spruce (*Picea rubens* Sarg.)-Fraser fir (*A. fraseri*) matrix (Russell, 1953; Whittaker, 1956).

In the Park, high-elevation deciduous hardwood forests extend to elevations of 1,680 m (Whittaker, 1956). These deciduous hardwood forests are comprised of four primary forest types: northern hardwood forests, high-elevation oak forests, forested boulderfields, and beech forests—combined, these forest types cover ~17% of the Park (34,109 ha; Jenkins, 2007). In these deciduous, high-elevation forests, north and northeast exposed sites are more mesic, dominated by *F. grandifolia* along with other mesic species such as mountain maple (*Acer spicatum* Lam.), yellow buckeye (*Aesculus flava* Aiton) and yellow birch (*Betula allegheniensis* Britton), while south, southwest, and westward exposed sites are more xeric, dominated by *F. grandifolia* in near monocultures (Whittaker, 1956). While more infrequent in the Park, in these sheltered, south-facing slopes, *F. grandifolia* can represent as much as 98% of the total basal area in a stand (Bratton, 1975).

These isolated, near monoculture stands of beech trees were locally called beech orchards prior to Russell's (1953) more specific description of them as 'beech gaps'. He further describes these 'beech gaps' as forests of nearly pure stands of *F. grandifolia* found on south-facing slopes at relatively high elevation (above 1,524 m). These south-facing slopes are usually found in east-west dips or on northeast-southwest ridges, having very abrupt boundaries with the adjacent spruce-fir matrix. This new, elevational-specific definition brought with it some ambiguity though; it appears to be primarily one of semantics, with the term 'beech gap' becoming popular in the context of GRSM publications. The term beech gap itself appears in multiple Park studies, with plot work within these forest types ranging from 1125 m to 1828 m (Whittaker, 1956; Wiggins et al., 2004; Taylor, 2006; Morris et al., 2014).

For the purposes of the present work, all plots were sampled in beech gaps as defined in the BBD Monitoring Protocol for GRSM, not per Russell's (1953), more specific, high elevation (above 1,524 m) definition. While *F. grandifolia* covers a wide range of elevations in GRSM (473 m at Grassy Branch to 1,781 m at Sweat Heifer), there are few of these high-elevation beech gaps (above 1,524 m, as per Russell's definition) in the Park (Ward, 1986; Blozan, 1995). Ashe (1922) estimated that pure beech type forests equate to less than 4,000 ha (10,000 ac) in North Carolina, and probably less in Tennessee.

Due to their restricted range, infrequent occurrence, and limited acreage across the landscape in the Southern Appalachians mountains, beech gaps 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 and hog rooting caused 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).

Fagus grandifolia trees grow to variable sizes in the Park, but in these beech gaps, the species rarely exceed 38 cm DBH, and typically appear as nearly pure stands (high densities) of small, stunted individuals (due to the root sprouting nature of *F. grandifolia*) in GRSM (Russell, 1953; Morris et al., 2014). In turn, these beech thickets can cast dense shade on the forest floor, thereby limiting recruitment of co-occurring tree and shrub species (Whittaker, 1956; Giencke et al., 2014), though phytotoxic effects of beech leaf leachate may also contribute to reduced recruitment within beech gaps (Hane et al., 2003). Instead, sedges, ferns, and other low-growing, shade-tolerant herbs thrive, particularly in south-facing beech gaps (Whittaker, 1956).

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). Surpassing GRSM, the BBD complex now extends southerly into Nantahala and Pisgah National Forests (United States Forest Service, 2014). In Tennessee, Monroe county represents

the furthest known distribution of the non-native beech scale (*C. fagisuga*), while its south easterly distribution through North Carolina has been more severe; traveling as far south as Cherokee county, and easterly into Clay, Macon, Jackson, Transylvania, and Henderson counties (Cale et al., 2017).

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 beech gaps. Over the course of 23 years, it is likely that these plots have experienced shifts in species composition, frequency, density, and basal area. Further, the loss of this foundational species within beech gaps, has the potential to displace many other species of wildlife such as bears, deer, wild boar, rodents, and bird species that depend heavily on the tree's ability to produce heavy mast years (Tubbs and Houston, 1990). 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 beech gap forest structure and composition at 10 plots established by GRSM personnel in 1994.

This goal will be assessed in four parts:

1. Overstory tree shifts in beech gap community structure and composition:

How has the loss (i.e., death) of mature *F. grandifolia* trees (associated with the arrival of BBD) within beech gaps contributed to spatial and temporal shifts in overstory forest structure and composition over the past 23 years?

2. Understory sapling influence: How have these overstory changes in beech plot attributes influenced understory species survival, and what compositional changes have occurred over time?

3. Woody seedling influence: Given the shifts in overstory tree structure and composition, is woody seedling regeneration showing a shift in woody seedling community composition?

4. Future direction of beech gaps in GRSM: Do these shifts in community structure and composition have implications for the long-term persistence of beech gaps?

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CHAPTER TWO

**MEASURING SPATIAL AND TEMPORAL SHIFTS
IN BEECH GAP FOREST STRUCTURE AND COMPOSITION
IN RESPONSE TO BEECH BARK DISEASE
IN GREAT SMOKY MOUNTAINS NATIONAL PARK**

ABSTRACT

PREMISE OF THE STUDY: 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 beech gaps, which are G-1 ranked (critically imperiled) communities where American beech (*Fagus grandifolia* Ehrh.) is a foundational tree species.

METHODS: In 1994, GRSM initiated the BBD Monitoring Protocol at 10 beech gap plots in the Park. Park service personnel subsequently sampled these plots biennially from 1994 to 2012 to investigate infestation patterns and host mortality. In 2017, all 10 plots were resampled following the BBD protocol. 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 (increases or decreases in absolute basal area) were analyzed using repeated measures linear mixed effects models (RMLMM).

KEY RESULTS: Beech gap 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, but over the 23-year study period, no significant change in total basal area was observed, indicating that the loss of mature *F. grandifolia* trees was compensated by co-occurring species.

CONCLUSIONS: Beech gaps have a limited distribution in GRSM. The loss of the foundational species, *F. grandifolia* (the dominant tree species which defines beech gaps), will have broad consequences for associated biota, ecosystem function, and potentially, the long-term persistence of beech gaps in GRSM.

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

In the eastern United States, forests have routinely 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.

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 (*Xylococcus 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 an introduced European fungus (*Neonectria faginata* (Pers.:Fr.) Fr. Var. Lohman, A. M. Watson, & Ayers), or a native fungus (*Neonectria ditissima* (Tulasne & C. Tulasne) Samuels & Rossman; Wiggins et al., 2004; Cale et al., 2015). Combined, the BBD complex has led to extensive mortality of *F. grandifolia* trees, decreases in net forest primary 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 aboveground 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). Both the non-native beech scale (*C. fagisuga*) and the introduced European fungus (*N. faginata*) are believed to have made their way into Halifax, Nova Scotia, circa 1890 on stocks of ornamental European beech trees (Wiggins et al., 2004).

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 can 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, beech gaps of Great Smoky Mountains National Park (GRSM; Figure 1; Wiggins et al., 2004; Cale et al., 2017).

Beech gaps of GRSM

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 1,680 m (Whittaker, 1956). These deciduous hardwood forests are comprised of four primary forest types: northern hardwood forests, high-elevation oak forests, forested boulderfields, and beech gap forests—combined, these forest types cover ~17% of the Park (34,109 ha; Jenkins, 2007). Beech gaps 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 1,781 m at Sweat Heifer), there are few of these high-elevation beech gaps (above 1,524 m, as per Russell's definition) in the Park (Ward, 1986; Blozan, 1995). Ashe (1922) estimated these forest types equate to less than 4,000 hectares in North Carolina, and probably less in Tennessee. Due to their restricted range, infrequent occurrence, and limited distribution across the Southern Appalachian Mountains, beech

gaps 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).

Exotic pests and pathogens in GRSM

In the Park, three long-term forest health monitoring programs have been implemented to document changes in forest structure and composition at the landscape level (Taylor, 2012). These monitoring programs have been implemented for: 1) balsam woolly adelgid (*Adelges piceae* Ratzeburg)—a non-native aphid-like insect that feeds on the trunks and limbs of Fraser fir (*Abies fraseri* (Pursh) Poir.) trees (implemented in 1986); 2) butternut canker (*Ophiognomonia clavignenti-juglandacearum* (Nair, Kostichka, & Kuntz) Broaders & Boland)—a non-native fungal disease that forms cankers along the trunks and stems of butternut trees (*Juglans cinerea* L.; implemented in 1987); and 3) BBD as described above (implemented in 1994). Monitoring programs become particularly crucial for host trees that have restricted habitat requirements and distributions (such as GRSM beech gaps) which are currently being impacted by BBD.

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 beech gaps 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 beech gaps throughout GRSM (Blozan, 1995; Taylor, 2006).

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 beech gaps. 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 beech gap forest structure and composition in 10 plots established by GRSM. Using spatial and temporal data collected in GRSM beech gaps since 1994, the goal was to assess 1) overstory tree shifts community structure and composition in GRSM beech gaps 2) the influence on understory saplings and woody seedlings, and 3) the future direction of beech gaps in GRSM.

METHODS

Field sampling

Plot establishment—In 1994, 10 permanent 20 m x 20 m (400 m² [or 0.04 ha]) plots were established in select beech gaps throughout GRSM (Figure 2). These 10 plots (Table 1) were sampled biennially from 1994-2012 by GRSM Park staff to monitor populations of *F. grandifolia* for BBD infestation, progression, and host mortality (Taylor, 2006). 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; Table 2; 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.

Overstory tree sampling—In 2017, within each plot (400 m² total sample area per plot; Figure 3), 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.

Understory sapling sampling—In 1994, each plot was further divided into four, 10 m x 10 m subplots (Figure 3). 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 x 8 m strip (Figure 3) 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; Figure 3) 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).

Woody seedling sampling—Nested further within each of the three 2 m x 8 m strips described above, a single 1 m x 1 m quadrat (Figure 3) 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; Figure 3) 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].

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.

Overstory trees basal area calculations—For each overstory tree, the basal area (BA) calculations below were conducted in Microsoft Excel. 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).

To calculate each tree's BA, its DBH (cm) must be first converted to a cross sectional area ($\text{m}^2 \text{ tree}^{-1}$) by use of the *foresters constant* as defined in equation (a), where g = tree cross sectional area (m^2) and $\pi = 3.14$. Thus, g (m^2) is expressed as a function of DBH in centimeters (Husch et al., 1982).

$$\text{a) } g (\text{m}^2) = \frac{\pi}{40,000} = 0.00007854 \quad (\text{Foresters constant})$$

Each tree's DBH (cm) value was then squared (cm^2) and multiplied by the forester's constant (from equation a) to obtain a cross-sectional BA value ($\text{m}^2 \text{ tree}^{-1}$) for each tree within a plot (equation b).

$$\text{b) } \text{Single tree's DBH (cm)}^2 \times 0.00007854 = (\text{m}^2 \text{ tree}^{-1}) \quad (\text{BA per tree})$$

Lastly, each tree's cross sectional BA value (from equation b) was divided by the total plot area sampled (i.e., 0.04 ha) to obtain each tree's BA per hectare ($\text{m}^2 \text{ ha}^{-1} \text{ tree}^{-1}$; equation c).

$$\text{c) } \frac{\text{Single tree/s BA (m}^2 \text{ tree}^{-1}\text{)}}{\text{Total plot area (0.04 ha)}} = (\text{m}^2 \text{ ha}^{-1} \text{ tree}^{-1}) \quad (\text{BA per hectare per tree})$$

Equation (c) effectively scales each tree's cross sectional BA value ($\text{m}^2 \text{ tree}^{-1}$) within a plot to a broader, landscape-level BA per hectare value ($\text{m}^2 \text{ ha}^{-1} \text{ tree}^{-1}$). 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.

Overstory trees community-level analyses—Using each species' relativized overstory tree BA per hectare data, a 'community observation x species matrix' was constructed to include all plots and all sampling years ($n = 110$; i.e., 10 plots x 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 x 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 x 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.

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. The same data used for the PERMANOVA analysis were used in the RMLMM analysis.

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,

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 (equation d; defined as the average number of individuals per unit area), relative frequency (equation e; defined as the percentage of plots occupied by a given species), and relative BA per hectare (equation f; defined as the dominance of each species per unit area) as described in (Kent, 2012).

$$\text{d) } \left(\frac{\text{the density of a given species}}{\text{the sum of the densities of all species}} \right) \times 100 \quad \text{(Relative density)}$$

$$\text{e) } \left(\frac{\text{the frequency of a given species}}{\text{the sum of the frequencies of all species}} \right) \times 100 \quad \text{(Relative frequency)}$$

$$\text{f) } \left(\frac{\text{the BA per hectare of a given species}}{\text{the sum of BA per hectare of all species}} \right) \times 100 \quad \text{(Relative BA per hectare)}$$

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 divided by three (Plocher, 1999), IV reported here are a true sum of the three percentages (each 100 maximum).

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. After multiple successful requests to Park personnel for the raw field data sheets (to fill in years of missing data), inconsistencies were still deemed too great for further statistical analyses. These faults could be attributed to the quality of data collection, rapidly changing climatic conditions, and/or changes in personnel over the 23-year study period.

RESULTS

Overstory trees

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 (Figure 4a). The trees belonged to 20 total species, summarized in Table 3. The number of live, overstory trees sampled varies by plot, by sample year, and by species (Figures 4a, 4b, 4c).

Abundance by plot—Overstory tree abundance (by plot) ranged from 49 to 142 trees (Figure 4a). Of the 923 total trees, Deep Creek represented the least number of individuals ($n = 49$), and Indian Gap represented the most ($n = 142$; Figure 4a). All remaining plots fell within these lower and upper limits.

Abundance by sample year—Overstory tree abundance (by sample year) ranged from 429 to 683 trees (Figure 4b). Of the 923 total trees, 1998 represented the least number of individuals ($n = 429$), and 2010 represented the most ($n = 683$; Figure 4b). 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 4; Figure 4b).

Abundance by species—Overstory tree abundance (by species) ranged from 7 to 650 trees (Figure 4c). Of the 923 total trees, *A. rubrum* represented the least number of individuals ($n = 7$), and *F. grandifolia* represented the most ($n = 650$; Figure 4c). While 20 total species were identified, only 10 of these species were found in three or more plots (Table 3) and are summarized in Figure 4c. 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 4). The remaining 10 species combined and analyzed as infrequent species decreased in abundance over the 23-year study period (Table 4).

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 5) on community composition. These results are visualized by NMDS in Figure 5, 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 (Figure 5). Community composition changed (i.e., ellipses elongation and widening due to changes in species relative BA per hectare) 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 (Figure 5).

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 (Figure 5). 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 (Figure 5).

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* (Figure 5). Fork Ridge and Newfound 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 Newfound Gap became more influenced by *A. rubrum*, *A. saccharum*, *B. lenta*, *B. allegheniensis*, and *P. rubens* (Figure 5). 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 (Figure 5). 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 (Figure 5).

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 4 and Figure 6. 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 4; Figure 6).

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* ($+3.51 \text{ m}^2 \text{ ha}^{-1}$; $p < 0.001$), followed by *H. tetraptera* ($+3.36 \text{ m}^2 \text{ ha}^{-1}$; $p = 0.015$), *A. saccharum* ($+2.94 \text{ m}^2 \text{ ha}^{-1}$; $p < 0.001$), *B. allegheniensis* ($+2.51 \text{ m}^2 \text{ ha}^{-1}$; $p = 0.001$), and *A. rubrum* ($+1.31 \text{ m}^2 \text{ ha}^{-1}$; $p < 0.001$; Table 4; Figure 6). Smaller, but significant increases in mean BA per hectare were also identified in *A. pennsylvanicum* ($+0.63 \text{ m}^2 \text{ ha}^{-1}$; $p < 0.001$) and *B. lenta* ($+0.64 \text{ m}^2 \text{ ha}^{-1}$; $p < 0.001$; Table 4; Figure 6).

No significant change in mean BA per hectare were identified for the 10 species combined and analyzed as infrequent species ($+1.26 \text{ m}^2 \text{ ha}^{-1}$; $p = 0.160$) and *A. spicatum* ($+0.30 \text{ m}^2 \text{ ha}^{-1}$; $p = 0.260$; Table 4; Figure 6). Lastly, analysis of total BA per hectare (all 20 species combined) indicated no significant change ($-5.41 \text{ m}^2 \text{ ha}^{-1}$; $p = 0.117$) over the 23-year study period (Table 4; Figure 6).

Shifts in importance—Of the 10 species identified in three or more plots (Table 3), *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 6; Figure 6). 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 6). The remaining 10 species combined and analyzed as infrequent species showed an inconsequential reduction in importance over the 23-year study period (Table 6).

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 6), 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.

Understory saplings

Due to numerous, detectable data entry inconsistencies on both the raw field data sheets and in the Microsoft Access database maintained by GRSM, understory

sapling data could not be statistically analyzed, beyond abundance and distribution summaries. A common fault identified in the understory sapling data was due to faulty sampling in the incorrect subplot (and/or subsequently, the incorrect 2 m x 8 m strip layout) during data collection intervals.

Total abundance—A total of 2392 live, understory 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 (Figure 7a). The trees belonged to 20 total species, summarized in Table 3. The total number of live, understory saplings sampled varies by plot, by sample year, and by species (Figures 7a, 7b, 7c).

Abundance by plot—Understory sapling abundance (by plot) ranged from 75 to 519 saplings (Figure 7a). Of the 2392 total saplings, Deep Creek represented the least number of individuals ($n = 75$), and Fork Ridge represented the most ($n = 519$; Figure 7a).

Abundance by sample year—Understory sapling abundance (by sample year) ranged from 98 to 441 saplings (Figure 7b). Of the 2392 total saplings, 1994 represented the least number of individuals ($n = 98$), and 1998 represented the most ($n = 441$; Figure 7b). All remaining sample years fell within these lower and upper limits.

Abundance by species—Understory sapling abundance (by species) ranged from one to 2030 saplings (Figure 7c). Of the 2392 total saplings, *B. lenta* represented the least number of individuals ($n = 1$), and *F. grandifolia* represented the most ($n = 2030$; Figure 7c). While 20 total species were identified (Table 3), data are only reported for the same 10 overstory tree species found in three or more plots (Table 3), plus the remaining 10 species combined and analyzed as infrequent species, summarized in Figure 7c.

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, woody seedling data could not be statistically analyzed, beyond abundance and distribution summaries. A common fault identified in the woody seedling data was due to faulty sampling in the incorrect subplot (and/or subsequently, the incorrect 2 m x 8 m strip and 1 m x 1 m quadrat layouts) during data collection intervals.

Total abundance—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 (Figure 8a). The trees belonged to 21 total species, summarized in Table 3. The total number of live, woody seedlings sampled varies by plot, by sample year, and by species (Figures 8a, 8b, 8c).

Abundance by plot—Woody seedling abundance (by plot) ranged from 9 to 127 seedlings (Figure 8a). Of the 584 total seedlings, Forney Ridge represented the least number of individuals ($n = 9$), and Sweat Heifer represented the most ($n = 127$; Figure 8a). All remaining plots fell within these lower and upper limits.

Abundance by sample year—Woody seedling abundance (by sample year) ranged from zero to 108 seedlings (Figure 8b). Of the 584 total seedlings, 1994 represented the least number of individuals ($n = 0$), and 1996 represented the most ($n = 108$; Figure 8b). All remaining sample years fell within these lower and upper limits.

Abundance by species—Woody seedling abundance (by species) ranged from zero to 375 seedlings (Figure 8c). 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 ($n = 375$; Figure 8c). While 21 total species were identified, data are only reported for the same 10 overstory tree species found in three or more plots (Table 3), plus the 11 species combined and analyzed as infrequent species, which are summarized in Figure 8c.

DISCUSSION

The loss of a foundational tree species in GRSM

In Great Smoky Mountains National Park (GRSM) beech gaps, 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 northeastern United States and Europe for over a century (Cale et al., 2017), the degree to which BBD has impacted GRSM beech gaps 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 in Evans et al., 2004).

GRSM currently represents a disjunct occurrence of the BBD complex and shifts in forest structure and composition have clearly occurred there. Beech bark disease is now well established in the Park and continues to threaten *F. grandifolia* trees within beech gap 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 beech gaps. 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 (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; Figure 2). 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.

As a foundational species in GRSM beech gaps, *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 beech gaps 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 beech gaps has contributed significantly to spatial and temporal shifts in forest structure and composition over the past 23-years. While not all plots have been affected the same, following the introduction of BBD into GRSM circa 1986, an ecosystem disturbance of this magnitude would not have otherwise been probable in the Park, short of anthropogenic influences. 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 beech gaps.

Direct impacts from the loss of overstory *Fagus grandifolia*

In GRSM, the number of mature (i.e., > 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 4). 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 $\sim 9 \text{ m}^2$ 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 4). 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 4). 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 4). While most of these species have been present in the plots since 1994 (except *Betula lenta*, which did not appear until 2008), 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 4). 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 hard-mast 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 oak 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 beech gaps 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).

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 beech gaps, while all remaining co-occurring species have become more important over the 23-year study period (Table 6). 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 beech gaps 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 beech gaps.

While reduced to smaller stemmed, stunted individuals by 2017, *F. grandifolia* remains as the most important overstory tree species in GRSM beech gaps, showing IV more than 4x that of the next two closest species, *Betula allegheniensis* and *A. saccharum* (Table 6). *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 beech gaps (Table 6), 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 beech gaps as of 2017 (Table 6). 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 beech gaps. Therefore, the reinfection of aftermath forests in GRSM remains as a threat, potentially leaving BBD as a long-term forest component in the Park.

Understory sapling and woody seedling response

While reciprocal replacement of *F. grandifolia* and *Aesculus flava* was identified for the overstory tree analyses, it appears that the understory response of GRSM beech gaps 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 (Figures 7c, 8c). *Fagus grandifolia* comprises 85% of all understory saplings (2030 of 2392 individuals; Figure 7c), and 64% of all woody seedlings (375 of 584 individuals; Figure 8c).

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 (Figure 7c). Combined understory sapling abundance (all species included) appear to have peaked in 1998, and generally declined through 2017 (Figure 7b).

With respect to woody seedlings, *Acer rubrum* and *A. saccharum* were the next most abundant species (i.e., > 20 individuals) relative to *F. grandifolia* (Figure 8c). While multiple *A. rubrum* woody seedlings were identified over the 23-year study period, their survival at these relatively high-elevations in GRSM beech gaps 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 (Figure 7c). Long-term successional patterns identified for woody seedlings in GRSM beech gaps (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.

Expected indirect ecological impacts of BBD in GRSM

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)

Once exotic forest pests invade an ecosystem, a cascade of effects is expected to manifest through many trophic levels (Crooks, 2002). Exotic forest pests not only produce physical shifts in forest structure and composition, they further alter forest ecosystems by influencing food and nesting availability for its inhabitants, thus, transforming animal communities, and even long-term, nutrient cycling processes. These modifications, along with the prominence of exotic species worldwide remains as one of the greatest threats to ecosystem function and biodiversity (Mooney and Hobbs, 2000; Karel and Man, 2017).

Fagus grandifolia, as an autogenic engineer influences both the physical and biotic properties of GRSM beech gaps. 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 Hellgren, 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). Beech masts are particularly important for many species of birds and mammals. Mice, squirrels, chipmunks, black bears, deer, and blue jays all utilize beechnuts as a palatable food source (Heyd in Evans et al., 2004). Following BBD infestations (and the subsequent loss of *F. grandifolia*), changes in populations of these fauna are likely to follow (Storer et al. in Evans et al., 2004).

Arboreal microhabitats include coarse woody debris (CWD) from dead treefall, which provide food, foraging and nest sites, and the facilitation of travel pathways for

species such as the white-footed mice (*Peromyscus leucopus*) in the southern Appalachian Mountains (Greenberg, 2002), and the cloudland deer mouse (*Peromyscus maniculatus*) in the Allegheny Mountains (Graves et al., 1988). Changes in animal behavior in BBD-affected plots will ultimately depend on how small mammals utilize the beech resource.

In GRSM, the loss of *F. grandifolia* from beech gaps, as an important hard mast species in high elevations is likely to further impact large mammal populations. Eiler et al., (1989) suggested the rate of black bear cub (*Ursus americanus*) reproduction in GRSM was largely dependent on the condition of the females, and thus these reproductive rates will be influenced by years of abundant fall masts by *F. grandifolia*. On top of this, the age of first reproduction in female black bears is also influenced by beechnut availability (Rogers, 1987). The loss of mature *F. grandifolia* trees in GRSM beech gaps is likely to deleteriously affect black bears in the Park, forcing them to forage elsewhere in the absence of these valuable fall food sources.

Fagus grandifolia is also an important food source for white-tailed deer (*Odocoileus virginianus*) which preferentially forage on beech sprouts during the winter and early spring months (Healy, 1971). This preferential foraging could lead to the movement of deer into higher elevations in the Park, causing further disturbances to an already critically-imperiled system. The ability of these animals to sustain the loss of mature, overstory *F. grandifolia* trees will ultimately depend on how the species rebounds from the shifts created by BBD's arrival into the Park.

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). However, in an old-growth hardwood forest in the Adirondack Mountains, McNulty and Masters in Evans et al., (2004) found that smaller trees appeared to be increasingly affected by BBD, which could potentially lead to a secondary killing front (Giencke et al., 2014).

The significant decrease in large DBH beech stems (and increase in smaller DBH stems) seen in GRSM has also been noted throughout the Adirondack region at elevations like those of GRSM plots (McNulty and Masters in Evans et al., 2004). This observed decrease, however, unexpectedly led to the production of more beechnuts, which researchers hypothesized was due to either 1) a greater number of young sprouts growing into reproduction age despite BBD-initiated stress, or 2) a greater number of small-to-medium trees per hectare, so that the cumulative result of fruiting increased beechnut production compared to beech forests containing only a few large individuals from 50-years ago (McNulty and Masters in Evans et al., 2004).

Future direction of beech gaps in GRSM

In GRSM, beech gaps have been dealing with BBD for at least 30 years (Ward, 1986). The BBD Monitoring Protocol sought to identify patterns of infestation, spread, and host mortality at 10 beech gap 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 beech gaps 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 inches] 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 beech gaps 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 inches) in GRSM beech gaps, 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.

While it is doubtful that BBD will have an effect as great as chestnut blight in GRSM, the reduction of larger DBH, mature overstory individuals to smaller DBH individuals is cause for concern. The elimination of mature beech from GRSM beech gaps 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 beech gaps, 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 beech gaps.

Challenges associated with long-term studies

The rates in which invasive pests are now spreading is unprecedented (Crooks, 2002). Shipping routes have expedited the influx of exotic species that now traverse the globe, leading to rapidly developing, broad, ecological consequences (Windle in Britton, 1997). Through long-term studies (LTS), complex ecological and evolutionary patterns (which may not appear in short-term studies), are becoming better understood (Kuebbing et al., 2018). LTS are important in advancing our known theories of forest pest and pathogen disturbances and their spread across the landscape.

Yet, LTS also come with a host of problems—from minor complications such as changes in personnel, inaccurate sampling, and lack of continuous funding—to larger problems, such as creating a study with too broad of a scope, failure to collect data at routine intervals, and using LTS to answer questions not appropriate to the study. For this reason, LTS are often underrepresented, underfunded, and underappreciated in the research community.

In GRSM, the BBD Monitoring Protocol has allowed for an assessment of forest change that would have otherwise been impossible due to the varying life stages in which *F. grandifolia* trees are impacted by the BBD complex. This monitoring protocol has become a powerful tool for the Park and has the potential to continue to contribute to a better understanding of BBD well into the future through continued sampling. Through the initiation of the BBD Monitoring Protocol, future forecasts for BBD spread, its impact on biota, and its consequences to these critically-imperiled forest communities could potentially help foresters lessen the impact of future invasions in the Park by other forest pests (Lewin, 1987).

Clearly though, improvements in LTS must be made—not only in sampling protocols and standardization of methods, but also in the research arena, funding structure, and continued commitment towards LTS (Likens, 1989). Open access to data is also of critical importance to better understand our changing ecosystems. The National Science Foundation’s National Ecological Observatory Network (NEON) is an exceptional effort to this end. Through access to data at larger, continental-scales, ecologists are better able to address scientific questions, characterize, and quantify changes once inaccessible to previous generations of ecologists (National Ecological Observatory Network, 2019). This can be accelerated by open source data networks provided by organizations such as NEON, USFS Forest Inventory and Analysis plots, and potentially even efforts driven by citizen scientists.

Future directions

BBD research is not heavily funded by government entities, so long-term efforts to track BBD-initiated changes are often undertaken by those with an interest in monitoring long-term changes in forest structure and composition. Due to this, many opportunities remain to learn more about this exotic disease complex, particularly, on efforts that investigate the cascade of indirect trophic effects as a result of BBD.

Since its arrival in the United States circa 1929, BBD research has been sporadic and heavily dependent on these individuals. It is surprising that BBD has received so little attention outside of the scientific community, since forest pests and pathogens (such as chestnut blight) have the ability to drive significant shifts across broad ecological scales, even generating impacts beyond that of climate change or air pollution (Lovett et al., 2006). While quantification of the physical state changes in overstory tree, understory sapling, and woody seedling structure and composition have been evaluated in this study, the abiotic shifts, and further influences on fauna in GRSM have yet to be investigated fully.

Further, there is remaining work to be done to better understand *F. grandifolia*'s resistance to *C. fagisuga*. Little is known about scale resistance, or how individuals obtain a potentially resistant trait (Koch et al., 2010; Čalić et al., 2017). Over a century of BBD research has helped to clarify scale dispersal mechanisms, patterns of infestation, and the impact on forest structure and composition, yet, BBD continues to spread, further impacting forest communities where *F. grandifolia* is a major forest component.

Ecologically, *F. grandifolia* influences the availability of resources to many other species, so the loss of this autogenic engineer will be noticeable through many trophic levels.

Considering the wide geographical range of *F. grandifolia*, a continued need for directed research will help to further quantify the landscape-level changes instigated by exotic forest pests and pathogens, potentially shedding light on future invasions.

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CHAPTER THREE

SUMMARY AND CONCLUSIONS

Since the arrival of BBD into GRSM circa 1986, the Park's beech gaps have seen drastic reductions in overstory tree basal area (> 50% loss) for the foundational tree species, *Fagus grandifolia*. This is problematic due to the tree's ability to produce mast years which support fauna dependent on fall nut production prior to overwintering. The basal area losses for this foundational tree species within a critically-imperiled forest community have led to significant shifts in forest structure and composition, potentially affecting biota reliant on *F. grandifolia*. Species composition in GRSM beech gaps has changed over the 23-year study period, with communities becoming more influenced by co-occurring species—particularly *Acer* and *Betula* species.

While *F. grandifolia* BA in the Park has been reduced drastically since 1994, the species remains as a dominant in the overstory tree, understory sapling, and woody seedling sampling classes designated in this study. The species has become less important since 1994, yet, *F. grandifolia* remains as the most important tree species within beech gaps as of 2017, showing importance values more than 4x that of the next closest species. This combined with the long-lived nature of *F. grandifolia*, and its ability to persist (for decades) in the dense shade of neighboring trees, leaves a promising outlook for the persistence of *F. grandifolia* within these beech gaps.

Table 1. GRSM long-term beech gap monitoring plot characteristics¹.

Plot name	Plot number	GPS coordinates ²	Number of <i>F. grandifolia</i> ³	Scale Density ⁴	Elevation (m)	Aspect
Sweat Heifer (SH)	01	35.62083° N, -83.40450° E	28	high	1781	SE
Jenkins Knob (JK)	03	35.56326° N, -83.55539° E	54	low	1654	N
Forney Ridge (FN)	04	35.52968° N, -83.50622° E	77	high	1530	W
Trillium Gap (TG)	06	35.67251° N, -83.43324° E	55	none	1435	W
Deep Creek (DC)	07	35.59868° N, -83.42718° E	31	none	1411	S
Indian Gap (IG)	09	35.60845° N, -83.43833° E	55	low	1625	S
Chimneys (CH)	10	35.62826° N, -83.46850° E	20	low	1125	NW
Fork Ridge (FK)	14	35.57713° N, -83.44916° E	35	high	1495	S
Newfound Gap (NG)	16	35.60933° N, -83.42199° E	49	low	1584	S
Gregory Bald (GB)	17	35.51953° N, -83.87042° E	45	none	1412	N

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

² Plot coordinates converted from Universal Transverse Mercator (UTM) to decimal degrees via www.geoplaner.com.

³ Number of overstory *F. grandifolia* trees in each plot > 3.5 cm DBH at time of plot installation (1994).

⁴ 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).

Table 2. Characterization of data collection over time (1994 – 2017).

	Taylor (1994-2012) Sampling ¹	Rumble (2017) Sampling ²
Overstory trees (sampled within entire 20 m x 20 m plots)		
Plot establishment	✓	✓
Species identification	✓	✓
Tagged trees	✓	–
DBH (cm; measured at DBH (1.37 m))	✓	✓
Life status	✓	✓
Crown class	✓	✓
Crown dieback	✓	✓
Crown defoliation	✓	✓
Scale rating	✓	–
Nectria rating	✓	–
Understory saplings (sampled within nested 2 m x 8 m strips)		
Species identification	✓	✓
Life status	✓	✓
Basal diameter (measured at 15 cm)	✓	✓
Woody seedlings (sampled within nested 1 m x 1 m quadrats)		
Species identification	✓	✓
Life status	✓	✓
Categorical classification of saplings	✓	✓

¹ Taylor sampling follows the BBD Monitoring Protocol for GRSM (Taylor, 2006).

² Rumble sampling shows deviations from the original, Taylor (2006) protocol. Due to time and sampling constraints, no new trees were tagged, and data for scale infestations (*C. fagisuga* or *X. betulae*) and fungal associations (*Neonectria* species) were not collected since these assessments require twice yearly monitoring due to the life stage of each organism.

Table 3. Overstory tree, understory sapling, and woody seedling species observed across 10 long-term beech gap 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</i> species ³	Maple sp.			✓
<i>Aesculus flava</i> Aiton	Yellow buckeye	✓	✓	✓
<i>Amelanchier laevis</i> Wiegand ^{1,2}	Allegheny serviceberry	✓	✓	
<i>Amelanchier</i> species ^{1,2}	Serviceberry sp.	✓	✓	
<i>Betula allegheniensis</i> Britton	Yellow birch	✓	✓	✓
<i>Betula lenta</i> L.	Sweet birch	✓	✓	✓
<i>Betula</i> species 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	✓		✓

Table 3 cont.

Scientific name	Common name	Overstory trees	Understory saplings	Woody seedlings
<i>Quercus rubra</i> L. ^{1,3}	Red oak	✓		✓
<i>Rhododendron catawbiense</i> Michx. ^{1,3}	Rhododendron	✓		✓
<i>Ribes</i> species 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 4. Change in overstory tree abundance and mean BA per hectare observed across 10 long-term beech gap monitoring plots over the 23-year study period (1994-2017).

Species	Number of Individuals		Mean BA per hectare ¹				
	1994	2017	1994	2017	Δ	p -value ²	
<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 overstory tree species not identified in at least three plots ($n = 10$; see Table 3).

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

Table 5. Permutational multivariate analysis of variance (PERMANOVA¹) results for community analysis.

	<i>df</i>	F.ratio	R ²	<i>p</i> -value
<i>Time</i>	1	71.856	0.02817	0.001
<i>Plot</i>	9	244.073	0.86114	0.001
<i>Time x plot</i>	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 x 11 species. Of the 11 species analyzed, one includes the combination of 10 species combined and analyzed as infrequent species (Table 3).

Table 6. Change in overstory tree importance values (IV)¹ observed across 10 long-term beech gap 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 3).

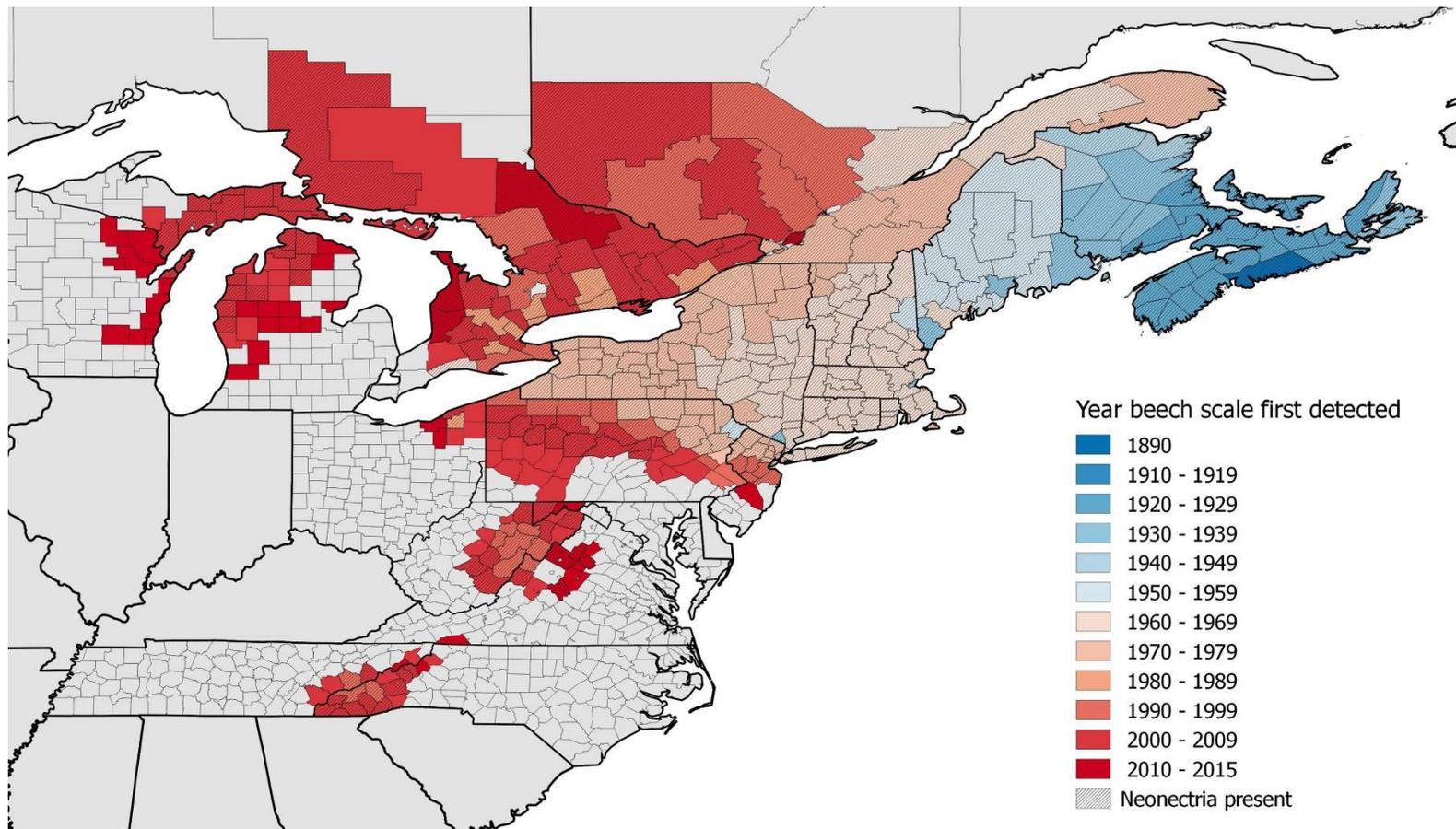


Figure 1. Beech bark disease complex map. County-level spread of beech scale (*C. fagisuga*) throughout North America since its 1890 introduction until 2015. County shading indicates the decade beech scale was first detected, whereas cross hatching indicates the current, reported range of *Neonectria* species. Map image reprinted from Cale et al., (2017). Beech bark disease in North America: Over a century of research revisited. *Forest Ecology and Management*, 394: 86-103. With permission from Elsevier (2019). Available at: <https://www.sciencedirect.com/journal/forest-ecology-and-management>.

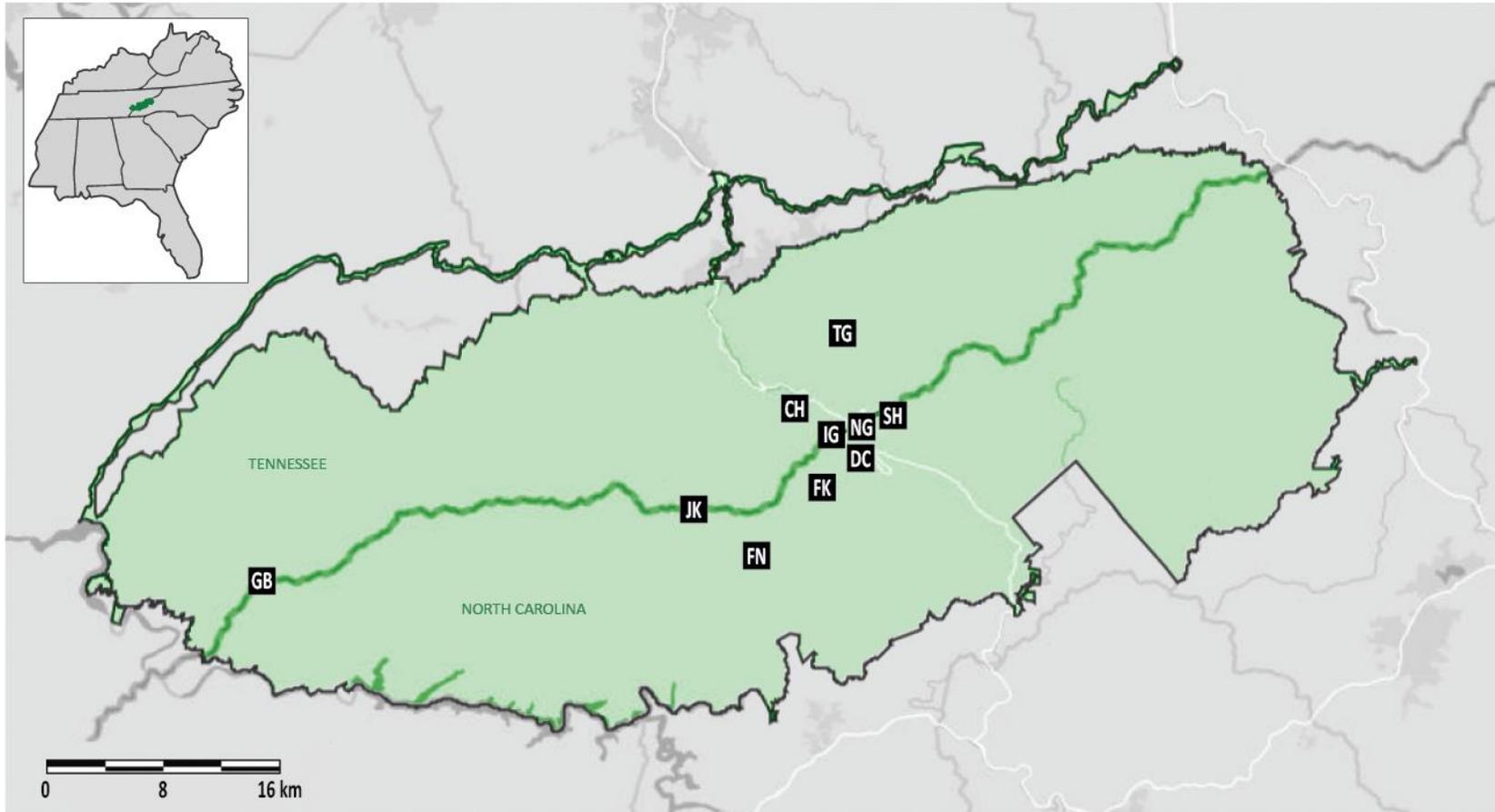


Figure 2. Location of 10 long-term beech gap monitoring plots in GRSM. Black dots represent plot location within the Park. Plot details are given in Table 1. SH = Sweat Heifer; JK = Jenkins Knob; FN = Forney Ridge; TG = Trillium Gap; DC = Deep Creek; IG = Indian Gap; CH = Chimneys; FK = Fork Ridge; NG = Newfound Gap; GB = Gregory Bald.

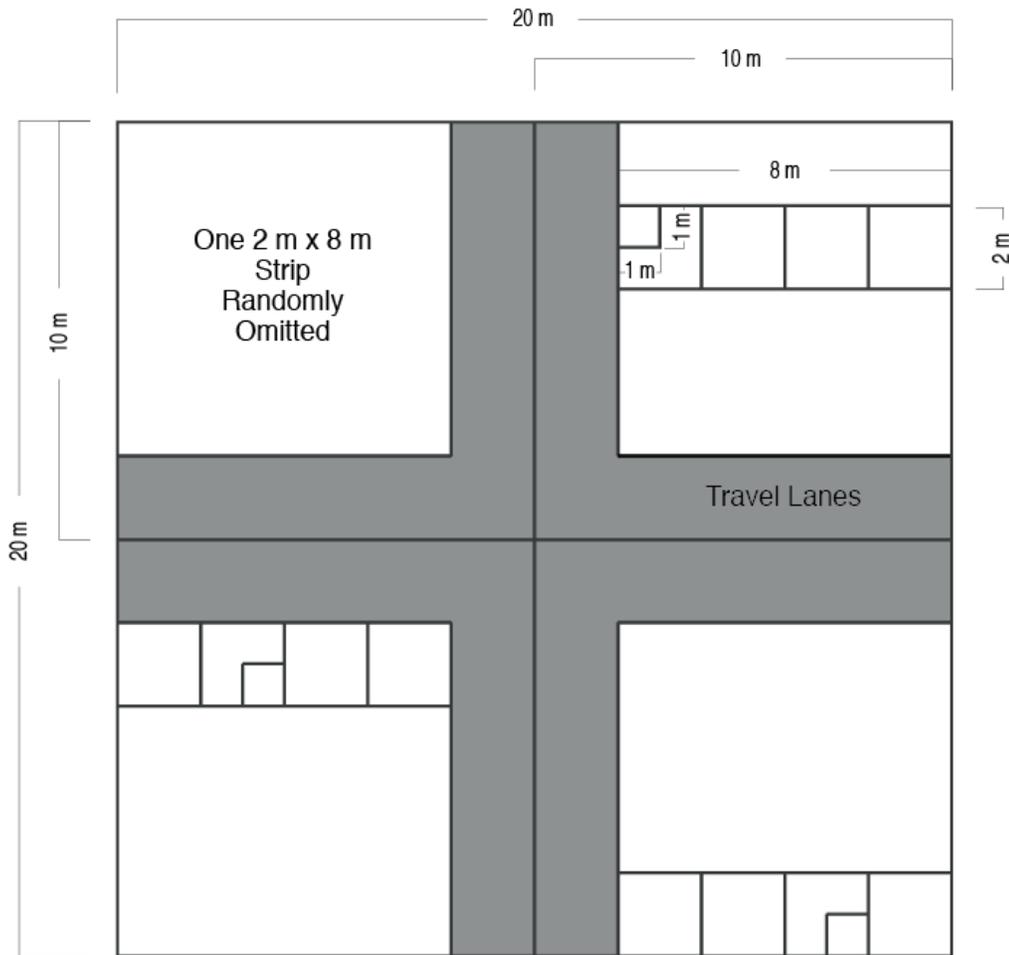


Figure 3. GRSM 20 m x 20 m (400 m²) long-term beech gap monitoring plot layout. Each 400 m² plot was further subdivided into: four, 10 m x 10 m subplots; three, 2 m x 8 m strips; and three, 1 m x 1 m quadrats to measure overstory and understory shifts in forest structure and composition over time.

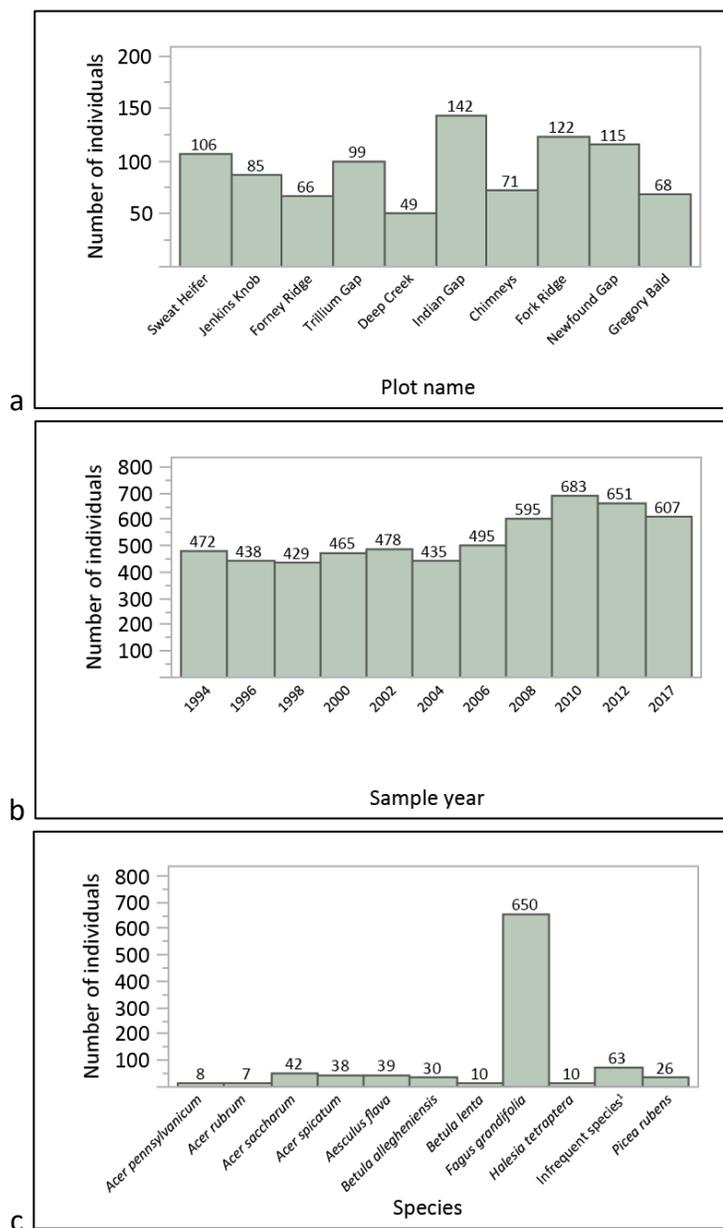


Figure 4. Abundance and distribution of live, overstory trees observed ($n = 923$) across 10 long-term beech gap monitoring plots over the 23-year study period (1994-2017).

Data organized by plot name (a), by sample year (b), and by species (c). Note y-axis scales vary across Figures 4a, 4b, and 4c.

¹ Infrequent species includes analysis of the 10 overstory species not identified in at least three plots (see Table 3).

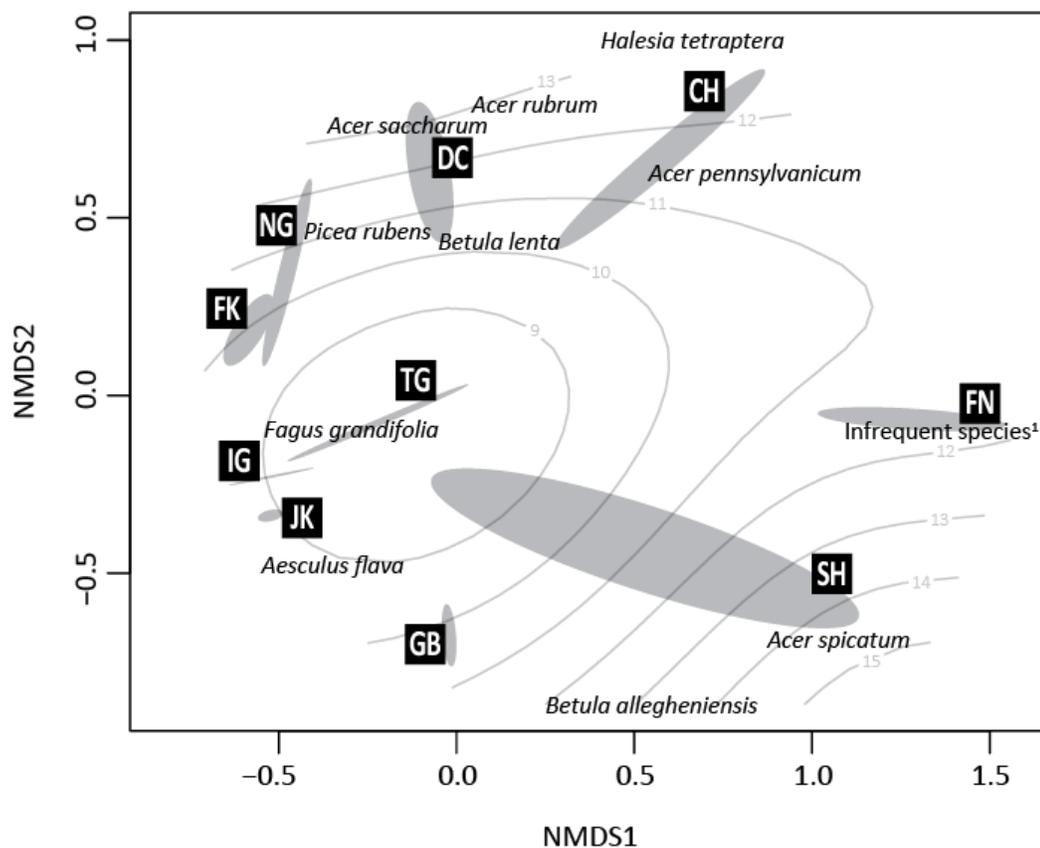


Figure 5. Non-metric multidimensional scaling (NMDS) visualization of PERMANOVA community analysis for overstory trees over the 23-year study period (1994–2017). The NMDS (2-D stress = 0.14) is based on species relative basal area for all overstory tree species identified in three or more plots ($n = 10$; see Table 3). Species not identified in at least three plots were combined and analyzed as infrequent species ($n = 10$; Table 3). 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.

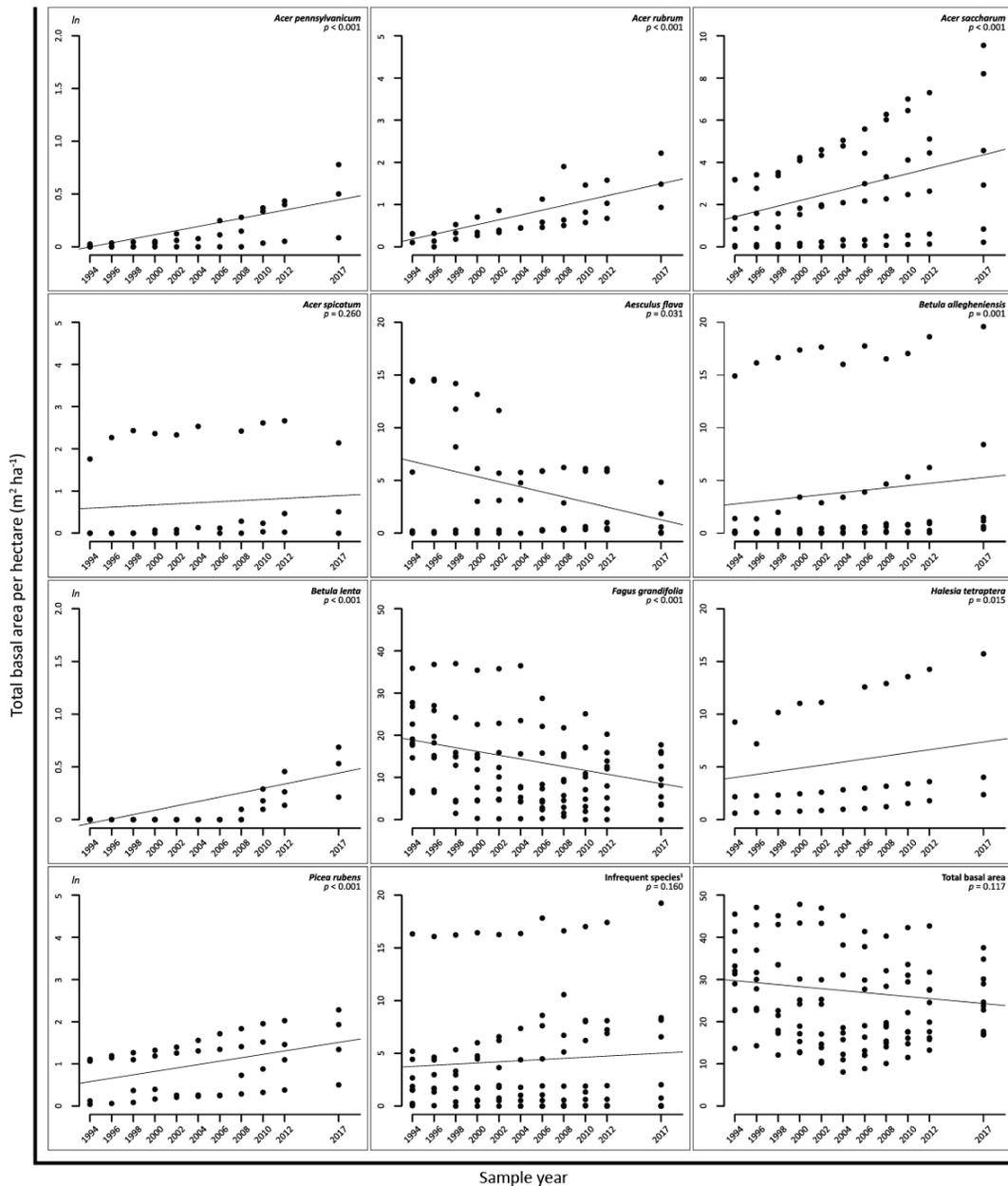


Figure 6. Overstory tree species-level analysis of basal area per hectare over the 23-year study period (1994-2017). Repeated-measures linear mixed effects models (RMLMMs) were conducted for the 10 species identified in three or more plots ($n = 10$; see Table 3), infrequent species not identified in at least three plots ($n = 10$; see Table 3), and total basal area which includes analysis of all 20 species combined. Note that data were \ln -transformed (plus 1) for *Acer pennsylvanicum*, *Acer spicatum*, and *Picea rubens* and scale of Y-axis varies by species.

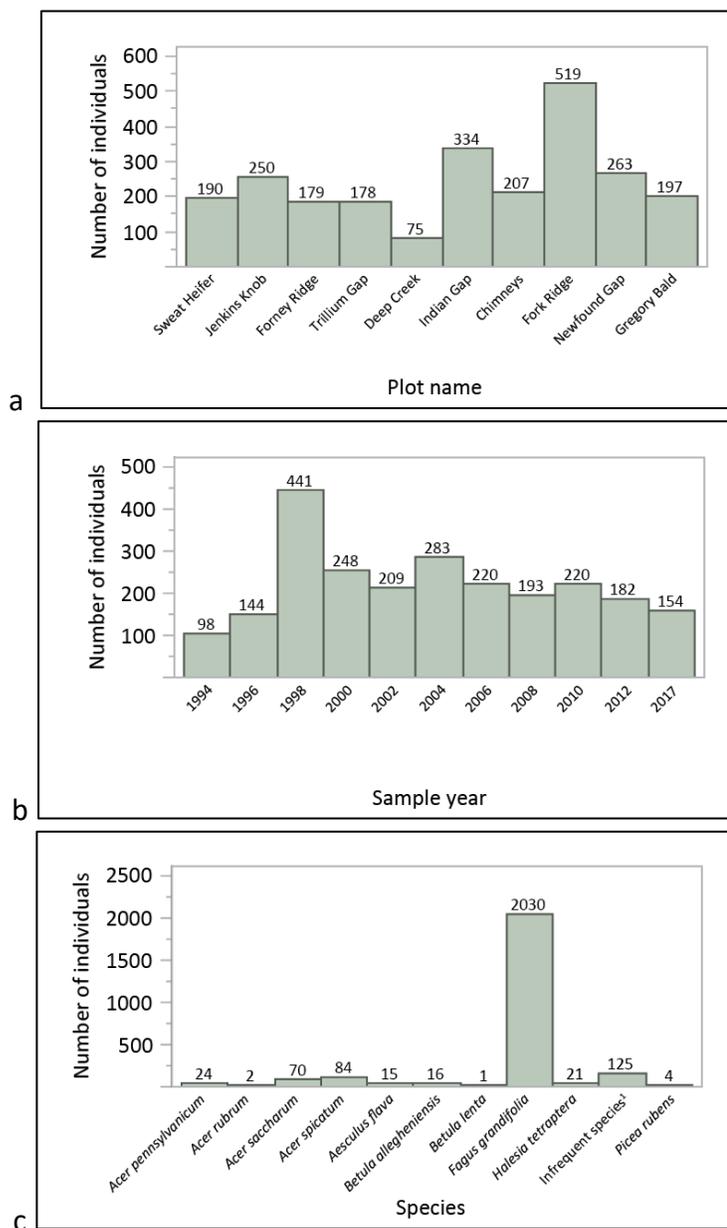


Figure 7. Abundance and distribution of live, understory saplings observed ($n = 2392$) across 10 long-term beech gap monitoring plots over the 23-year study period (1994-2017). Data organized by plot name (a), by sample year (b), and by species (c). Note y-axis scales vary across Figures 7a, 7b, and 7c.

¹ Infrequent species includes the 11 understory species not identified in at least three plots (see Table 3).

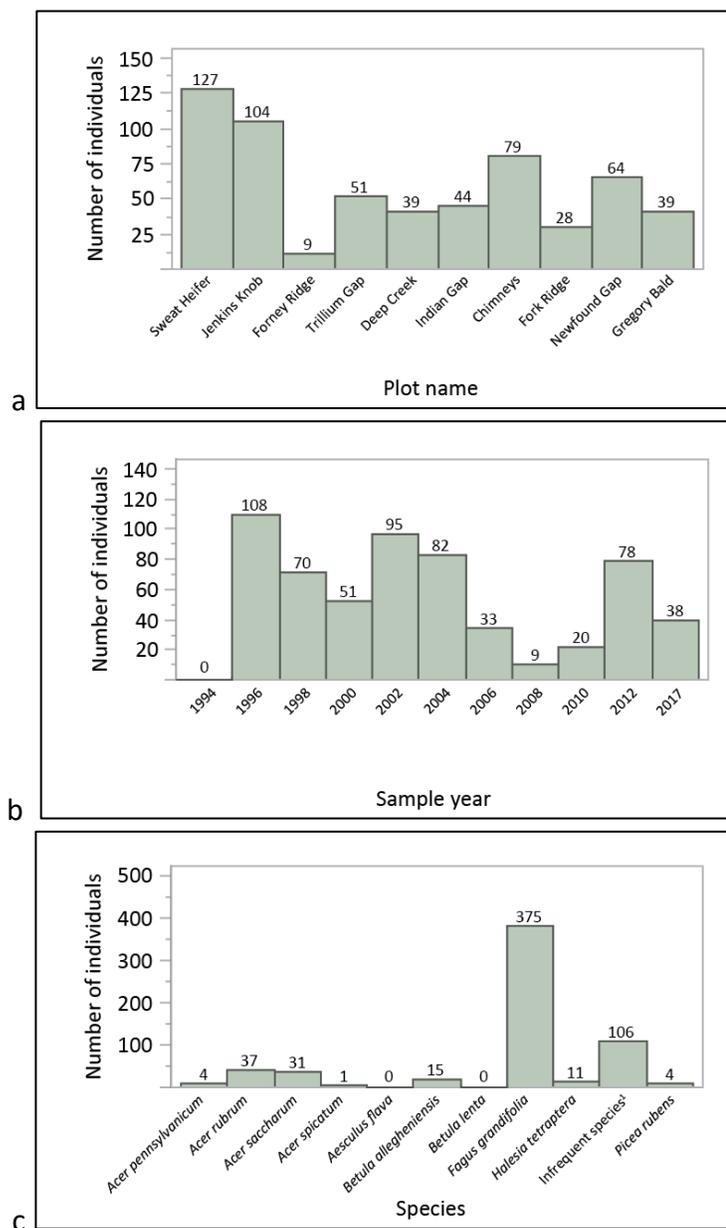


Figure 8. Abundance and distribution of live, woody seedlings observed ($n = 584$) across 10 long-term beech gap monitoring plots over the 23-year study period (1994-2017). Data organized by plot name (a), by sample year (b), and by species (c). Note y-axis scales vary across Figures 8a, 8b, and 8c.

¹ Infrequent species includes the 11 understory species not identified in at least three plots (see Table 3).