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The Great Smoky Mountains National Park All Taxa Biodiversity Inventory: A Search for Species in Our Own Backyard
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Vegetation Communities of Great Smoky Mountains National Park

Michael A. Jenkins*

Abstract - Great Smoky Mountains National Park (GSMNP) contains one of the most diverse assemblages of vegetation communities in North America. Over 70 unique community associations comprised of over 1300 native plant species have been identified in the Park. This wide array of communities provides habitat for unknown multitudes of other taxa whose abundance, distribution, and ecological importance remain largely unknown. The All Taxa Biodiversity Inventory (ATBI) underway in the Park is the first comprehensive attempt to better understand the vast array of species present in the Park. This paper discusses the composition, structure, distribution, and extent of vegetation communities in GSMNP. Detailed assessments of the vegetation, site, and soil characteristics of the 19 ATBI plots are also included.

Introduction

Great Smoky Mountains National Park (GSMNP) is internationally renowned as a center of biodiversity within North America. Complex ecological gradients combine to create a diverse mosaic of biological communities. Elevations in the Park range from 267 to 2025 m with 16 peaks greater than 1830 m. Topography is generally rugged and includes level valleys, gentle to steep side slopes, incised drainages, talus slopes, and rocky summits. The geology of the Great Smoky Mountains is extremely complex and often highly variable over short distances. The bedrock is dominated by metamorphosed sandstone, but acid-bearing slates, mafic and ultramafic rock, and tectonic windows underlain with limestone also occur (Southworth et al. 2005). This complex geology results in equally variable soils, which for the first time are being comprehensively studied and mapped in GSMNP. Annual rainfall varies from 140 cm at low elevations to over 200 cm on some high peaks.

The biological importance and diversity of GSMNP led to its designation as an International Biosphere Reserve in 1976 and World Heritage Site in 1983. Although the ATBI has helped highlight the diversity of many taxa in GSMNP, the Park has long been viewed as a center of vascular plant diversity in North America. White et al. (2003) identified 79 unique vegetation communities or associations in GSMNP. These communities are comprised of over 1600 species of vascular plants, of which less than a quarter are exotic

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(NPS 2006). The Park also contains 86 vascular plant species endemic to the southern Appalachians (White 1982), over 80 state-listed species (Bailey 2004, Franklin and Finnegan 2004), and 2 federally listed species (Franklin and Finnegan 2004). In addition to its rich mix of vegetation communities, GSMNP also contains one of the largest tracts of primary forest (a forest that has never been logged and has developed following natural disturbances and under natural processes) in eastern North America. Over 20% of the Park was never cleared of timber (primary forest; Fig. 1), and these forests include stands of old-growth that contain some of the largest trees in eastern North America. According to the *National Register of Big Trees* (American Forests 2007), national champion trees of 13 species including *Tsuga canadensis* (L.) Carr. (eastern hemlock), *Picea rubens* Sarg. (red spruce), and *Acer rubrum* L. (red maple) are found in GSMNP.

Despite its large size (>200,000 ha) and protected status, numerous biotic and abiotic factors have altered and continue to threaten vegetation communities within GSMNP. Among biotic factors, exotic species (including disease, insects, and plants) have been the most destructive. During the 1930s, *Cryphonectria parasitica* (Murrill) Barr (chestnut blight) virtually

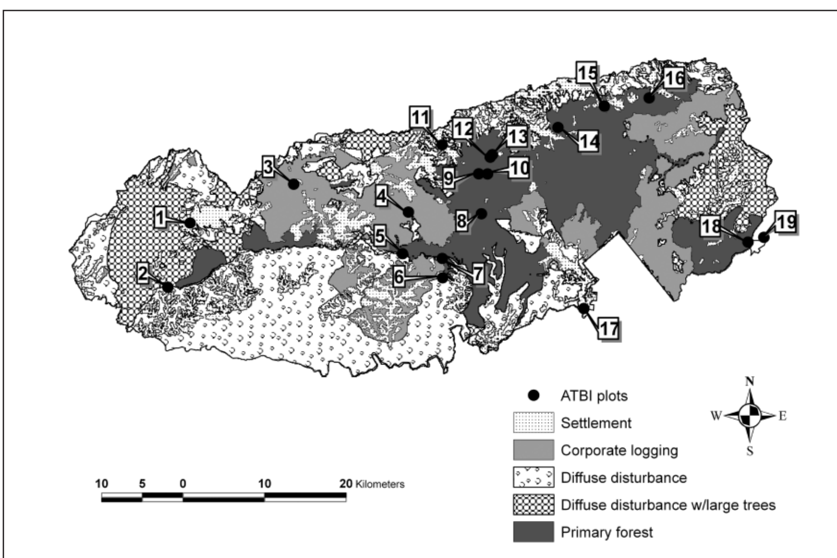

Figure 1. Location of ATBI plots within anthropogenic disturbance types delineated by Pyle (1988). 1 = Cades Cove, 2 = Gregory Bald, 3 = Tremont, 4 = Goshen Prong, 5 = Double Springs Gap, 6 = Andrews Bald, 7 = Clingmans Dome, 8 = Indian Gap, 9 = Mount LeConte-West Point, 10 = Mount LeConte-Boulevard, 11 = Twin Creeks, 12 = Trillium Gap, 13 = Brushy Mountain, 14 = Ramsay Cascade, 15 = Albright Grove, 16 = Snake Den Ridge, 17 = Oconaluftee, 18 = Cataloochee, 19 = Purchase Knob. Purchase Knob was not included in the analyses of Pyle (1988).

eliminated *Castanea dentata* (Marsh.) Borkh. (American chestnut) from the forest landscape of eastern North America. Since it was first discovered in 1954 (Speers 1958), *Adelges piceae* (Ratzeburg), the balsam woolly adelgid, has decimated *Abies fraseri* (Pursh) Poir. (Fraser fir) populations in high-elevation spruce-fir forests (Jenkins 2003, Smith and Nicholas 1998), and *Adelges tsugae* Annand (the hemlock adelgid) is already impacting eastern hemlock in the Park. Since the late 1980s, *Discula destructiva* Redlin, a pathogenic fungus that causes dogwood anthracnose, has killed *Cornus florida* L. (flowering dogwood) trees throughout the Park, and mortality has exceeded 90% in some forest types (Jenkins and White 2002). Over the past decade, beech bark disease, an insect/fungus complex, has decimated *Fagus grandifolia* Ehrh. (American beech) trees in high-elevation hardwood forests (Vandermast 2005). Although the population has been reduced since the 1970s, *Sus scrofa* L. (European wild boar) continues to alter understory vegetation within the Park. Currently, GSMNP actively controls around 50 exotic plant species that are known to displace native species, hybridize with natives, or interfere with cultural landscapes (Kristine Johnson, GSMNP Vegetation Management Specialist,Gatlinburg, TN, pers. comm.).

Native ungulates also exert considerable influence on the composition and structure of native vegetation. A lack of effective population control often leads to extremely high population densities and heavy herbivory that result in the degradation of vegetation communities (Rooney et al. 2004). In the woodlots and surrounding forests of Cades Cove, *Odocoileus virginianus* Zimm. (white-tailed deer) have altered the cover, diversity, and population demographics of forest herbs (Webster et al. 2005a) and suppressed tree regeneration (Griggs et al. 2006). In 2001, *Cervus elaphus* Erxleben (elk) was reintroduced in GSMNP. If this species is successfully reestablished, it may have considerable effects on a wide range of vegetation communities throughout the Park.

Alterations in the Park's disturbance regimes have also impacted vegetation communities. Throughout the Park, plant communities continue to recover from past unregulated logging and agricultural use (Pyle 1988, Webster et al. 2005b). Fire suppression has allowed the succession of numerous pine stands to hardwood dominance. In the absence of fire, succession towards hardwoods is accelerated by mortality caused by *Dendroctonus frontalis* Zimmermann (southern pine beetle; Coulson et al. 1999). Within hardwood stands, oak species are not regenerating under closed canopies on mesic sites (Jenkins and White 2002). The recently implemented prescribed burning program within the Park is counteracting many of these successional changes, but the full effect of fire on species composition and stand structure must be evaluated.

Among abiotic factors, inputs of air-borne pollutants have been well documented for over two decades and are likely impacting vegetation communities at high elevations. In GSMNP, research has shown that elevated ozone levels have negative impacts on 25 species of plants (Chappelka and Samuelson 1998). Although difficult to quantify, deposition of sulfur dioxide, nitrogen oxides, and particulate matter may impact vegetation communities by acidifying soils in susceptible areas, resulting in greater aluminum toxicity and cation leaching (Cronan and Schofield 1990, Huntington 2000).

A long succession of researchers have examined the distribution and underlying gradients of the complex mixture of vegetation communities that occur in GSMNP (Cain 1930, 1931; Golden 1981; MacKenzie and White 1998; White et al. 2003; Whittaker 1956). In one of the earliest studies, Cain (1931) examined the effects of soil acidity on the distribution of plant species and vegetation communities within the Park. In a paper that greatly influenced subsequent work, Whittaker (1956) examined the role of complex environmental gradients, including elevation and topography, on the distribution of vegetation communities. The vegetation types delineated by Whittaker (1956) have served as the starting point for subsequent classification efforts in GSMNP (Golden 1981, White et al. 2003). The conservation organization NatureServe created a vegetation classification of GSMNP that draws from the International Classification of Ecological Communities (ICEC), a system developed by ecologists from NatureServe and The Nature Conservancy to describe, classify, and rank specific ecological community types (White et al. 2003). Like many federal agencies, the National Park Service has adopted the ICEC as its standard for the classification and description of vegetation. This hierarchal classification developed for GSMNP describes 79 vegetation communities (or associations) and ranks them based upon rarity and threats. This classification has proven to be an invaluable resource for conservation planning, environmental impact analysis, and ecological research.

In this paper, I describe the vegetation communities of Great Smoky Mountains National Park. The species composition, site characteristics, and extent of major vegetation types are described. In addition, more detailed descriptions of the species composition, stand structure, coarse woody debris, and soil chemistry of the 19 ATBI plots (Fig. 1, sampling methods discussed below) are provided.

Methods used to sample ATBI plots

Between June and August of 1999, nineteen ATBI sites were established to develop and test sampling methodologies. These sites were selected to represent the range of vegetation communities that occur across the Park. At each ATBI site, a large area was delineated (typically 1 ha) to serve as a sampling and collecting area for ATBI researchers. Within each of these areas, either a 0.1-ha (20-m x 50-m) or 0.2-ha (40-m x 50-m) permanent vegetation plot was established. The larger plot size was used in the three old-growth forest sites (Albright Grove, Cataloochee, Ramsay Cascade) to better capture the variability of canopy trees; all other sites were sampled with a 0.1-ha plot. On forested plots, the dbh of all living and dead stems

<10 cm dbh were tallied by species into 4 dbh classes: 0.1–0.9 cm, 1.0–2.4 cm, 2.5–4.9 cm, and 5.0–9.9 cm. The dbh of all living and dead stems ≥10 cm was measured and recorded by species. Seedling density was recorded in four 10-m^2 (3.16-m x 3.16-m) subplots distributed across the 0.1-ha plot (eight subplots were used within 0.2-ha plots). The percent cover of all species was visually estimated in four 100-m^2 (10-m x 10-m) modules embedded within the larger 0.1-ha plot (eight modules were sampled within 0.2-ha plots). The length and midpoint diameter (MPD) of all down deadwood (DDW) with a MPD of ≥10 cm were also measured. Only portions of DDW ≥10 cm diameter and located within the plot were measured. Samples of the soil A-horizon (approximately 10 cm depth) were collected from across the ATBI sites. The basal area of living and dead trees and the volume of DDW were calculated for each plot and converted to a per hectare basis (presented in Table 1 and Fig. 2).

Vegetation Communities of Great Smoky Mountains National Park

Because of the variety and complexity of vegetation communities in GSMNP, a comprehensive discussion of individual communities is beyond the scope of this paper. Although White et al. (2003) identified 79 unique vegetation communities, for the purpose of this discussion I have grouped these associations into 11 major types comprised of 8 forested (montane

Table 1. Anthropogenic disturbance history, down deadwood (DDW) volume, and basal area of standing deadwood (SDW; snags) on the 19 ATBI plots established in 1999. Anthropogenic disturbance is based upon Pyle (1988).

Site	Anthropogenic disturbance history	DDW volume (m^3 ha^{-1})	SDW basal area (m^2 ha^{-1})
Clingmans Dome	Undisturbed	Not sampled	30.5
Mt. LeConte- Boulevard	Undisturbed	119.6	28.4
Mt. LeConte-West Point	Undisturbed	199.1	29.1
Double Springs	Diffuse	23.4	3.1
Indian Gap	Undisturbed	25.6	2.4
Trillium Gap	Undisturbed	22.8	4.0
Andrews Bald	Settlement	1.5	1.4
Gregory Bald	Settlement	Absent	Absent
Brushy Mt.	Undisturbed	Absent	Absent
Albright Grove	Undisturbed	164.4	9.6
Cataloochee	Undisturbed	182.5	1.5
Ramsay Cascade	Undisturbed	74.0	2.1
Snake Den Ridge	Undisturbed	134.8	2.1
Goshen Prong	Corporate logging	15.5	2.0
Oconaluftee	Settlement	28.4	2.7
Purchase Knob	Logging[1]	29.9	1.8
Tremont	Corporate logging	126.1	1.6
Twin Creeks	Settlement	17.0	2.4
Cades Cove	Settlement	Absent	Absent

[1]Purchase knob was not included in the land-use history by Pyle (1988). Based upon the history of western North Carolina and contemporary stand conditions, this site was most likely logged.

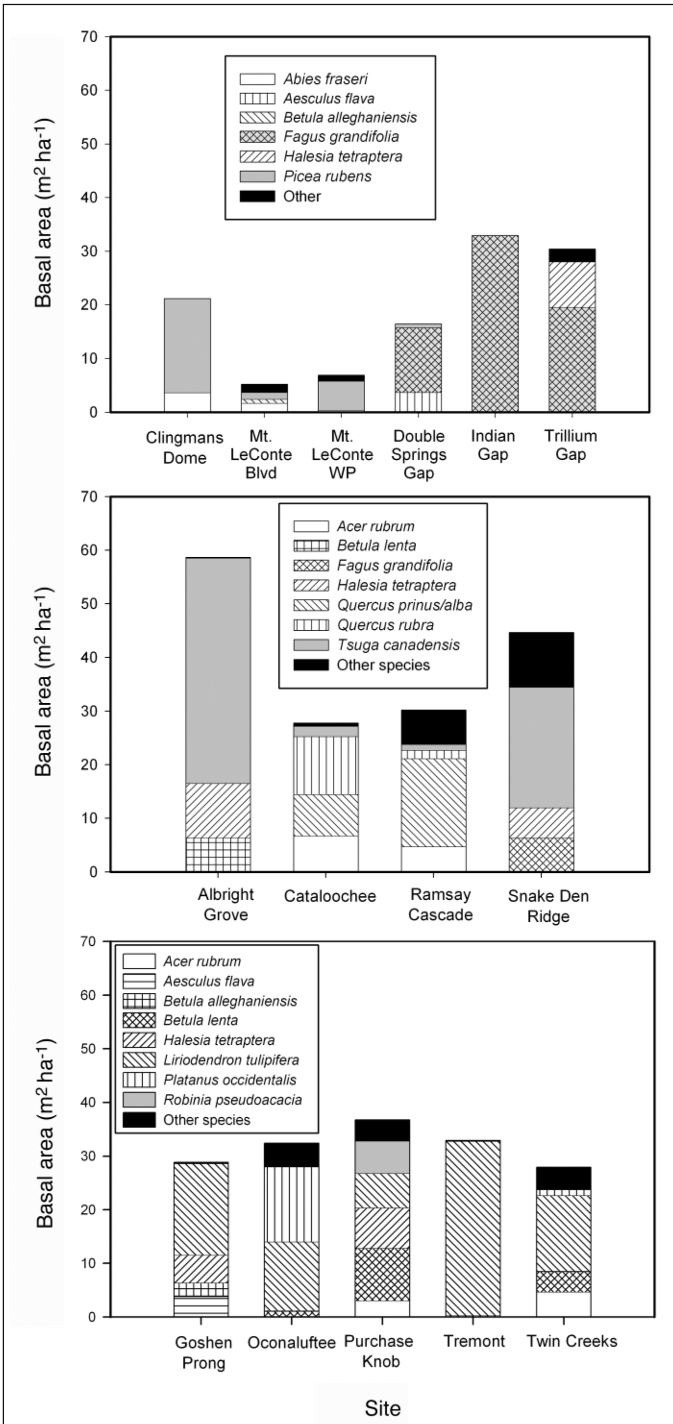

Figure 2. Overstory basal area of living trees on 14 forested ATBI plots. Plots are grouped as follows: (A) mid-to-high-elevation forests, (B) mid-elevation primary forest, and (C) low-to-mid-elevation secondary forest. Vegetation data were not collected on the Brushy Mountain ATBI plot.

alluvial forests, early successional forests, cove forests, hemlock forests, montane oak-hickory forests, xeric ridge forests, high-elevation hardwood forests, and spruce-fir forests) and 3 non-forested types (heath balds, grassy balds, and pasture). Associations were grouped into these types based upon similarities in species composition, landscape position, and management issues.

Montane alluvial forest

According to White et al. (2003), this forest type (comprised of 4 associations) occurs within the narrow rocky floodplains and islands of medium-sized rivers below 915 m elevation. The canopy of this forest type in GSMNP typically contains *Platanus occidentalis* L. (American sycamore) in varying amounts. Other overstory species include *Liriodendron tulipifera* L. (tulip-poplar), eastern hemlock, and *Betula* (birch) species. *Rhododendron maximum* L. (rosebay rhododendron) and *Leucothoe fontanesiana* (L.) Gray (dog-hobble) typically dominate the shrub layer, which may be quite dense along smaller streams and more narrow drainages. The shrub layer is often less developed in forests along large rivers in GSMNP, such as the Little River, Little Pigeon River, and Oconaluftee River. Herbaceous species composition is quite variable in this forest type and can be very patchy where shrubs dominate.

Montane alluvial forests are naturally uncommon in the southern Appalachians because they occupy a very discrete landscape position. For example, according to Madden et al. (2004), this forest type covers approximately 1%

Table 2. Total cover, percent of Park area, and NatureServe associations of 12 broad vegetation types in Great Smoky Mountains National Park (GSMNP).

Vegetation type	Total cover (ha)	Percent of Park area	Associations[A]
Acid cove forests	8912	4.3	7543, 7693
Cove hardwood forests	25,130	12.2	7695, 7710, 7878
Early successional forests	10,295	5.0	2591, 7219, 7879, 7944
Heath balds	2613	1.3	3814, 7876
Hemlock forests	4089	2.0	7102, 7136
High-elevation hardwood forests	34,109	16.6	4973, 4982, 6124,6130,6246,7285, 7295, 7298, 7299, 7300, 7861
Montane alluvial forest	2579	1.3	4420, 4691, 7339, 7880
Montane oak-hickory forest	64,566	31.3	6192, 6286, 7230, 7240, 7267, 7691, 7692, 8558
Pasture, old fields, grassy balds	943	0.5	4048, 4242
Spruce-fir forest	15,514	7.5	3839, 4983, 6049, 6256, 6272, 6308,7130, 7131
Xeric ridge forests	33,331	16.2	3560, 6271,7078,7097,7100,7119, 7493,7517, 7519
Other	4005	1.9	Numerous

[A]Vegetation types are based upon Ecogroups developed by NatureServe. Full association descriptions are provided in White et al. (2003). Coverages were estimated using the vegetation map of GSMNP created by Madden et al. (2004). Because some associations cannot be discerned from aerial photographs, the vegetation map does not include all listed associations.

of GSMNP (Table 2). Most montane alluvial forest in the Park occurs along smaller streams; the amount of this type that occurs within the floodplains of larger streams is considerably less. In addition, many areas of this forest type have been lost outside the Park due to agriculture and development. This community type is further threatened by road building and alterations to hydrology (White et al. 2003). Consequently, well-developed examples are rare, and existing forests of this type are a conservation priority.

The Oconaluftee ATBI plot is located in montane alluvial forest. The canopy of this site is dominated by *Platanus occidentalis* and *Liriodendron tulipifera* (Fig. 2), but also contains *Quercus imbricaria* Michx. (shingle oak) and *Juglans cinerea* L. (butternut: a rare species that has been heavily impacted by *Sirococcus clavigignenti-juglandacearum* Nair, Kostichka & Kuntz [butternut canker]). Because of the presence of *Q. imbricaria*, this site is classified as *Platanus occidentalis-Fraxinus pennsylvanica-Quercus imbricaria* Forest, a variant of montane alluvial forest (White et al. 2003). The shrub layer at this site is rather sparse, but the herb layer is quite species rich. Overall, this plot had a high richness of vascular plant species; total richness across all strata was 100 species. However, six of these species were exotic. Despite historically intensive land use (Table 1), this site still

Table 3. Site and soil characteristics of the 19 ATBI plots established in 1999. OM = organic matter, CEC = cation exchange capacity.

Site	Elevation (m)	Aspect	Slope (%)	Soil pH	Soil OM (%)	CEC	Ca/K/Mg saturation (%)
High-elevation spruce-fir forest							
Clingmans Dome	1956	98	32	3.6	3.9	8.4	7.0/1.5/3.0
Mt. LeConte-Boulevard	1978	45	15	3.6	3.8	7.4	6.8/1.2/2.4
Mt. LeConte-WP	1912	10	33	3.5	3.8	8.2	12.7/1.9/4.8
Mid-to-high-elevation beech forest							
Double Springs	1685	20	60	3.4	2.8	7.0	9.5/1.6/3.3
Indian Gap	1634	143	48	3.4	3.5	6.6	13.5/2.9/4.1
Trillium Gap	1429	285	47	3.5	3.5	8.0	9.5/2.2/3.0
Grassy and heath balds							
Andrews Bald	1757	NA	NA	4.4	3.5	7.9	5.8/2.4/3.2
Gregory Bald	1506	NA	NA	4.0	3.9	9.5	7.8/2.4/3.2
Brushy Mt. (heath)	1468	135	24	3.7	4.4	8.3	6.9/2.0/4.2
Low-to-mid-elevation primary forest							
Albright Grove	1033	353	36	3.5	3.9	10.0	11.3/2.5/3.0
Cataloochee	1385	188	32	4.8	3.8	7.8	13.8/2.7/3.8
Ramsay Cascade	935	220	36	4.0	3.5	7.2	7.3/2.6/3.9
Snake Den Ridge	932	20	60	3.5	3.9	8.8	15.5/1.8/2.9
Low-to-mid-elevation secondary forest							
Goshen Prong	917	11	12	4.1	3.0	8.7	19.7/2.7/4.0
Oconaluftee	612	NA	NA	4.7	2.3	6.9	33.1/3.5/6.8
Purchase Knob	1324	165	23	4.5	3.5	8.9	15.7/2.5/4.0
Tremont	544	28	35	5.7	3.0	12.3	62.1/2.1/9.0
Twin Creeks	594	311	10	4.8	3.1	8.1	20.5/2.8/6.6
Old field							
Cades Cove	522	NA	NA	5.7	2.6	8.8	48.4/2.7/10.9

had relatively high cation (Ca, K, Mg) saturation values (Table 3). Due to rapid decomposition and regular flooding, this site had the lowest percent organic matter (OM) of any site (2.3%). This lack of organic matter likely resulted in low overall cation exchange capacity (CEC = 6.9) compared to other low-elevation sites.

Early successional forests

This very common forest type is comprised of 4 associations that regenerated on abandoned agricultural land or heavily logged forests (Fig. 1) and covers over 10,000 ha in the Park (5% of total park area; Table 2). As its name suggests, this forest type is transitional on the landscape and is dominated by early successional species such as *L. tulipifera*, *Robinia pseudoacacia* L. (black locust), and *Pinus virginiana* P. Mill. (Virginia pine). Other canopy species may include *A. rubrum*, *Pinus strobus* L. (white pine), and *Betula lenta* L. (black birch). Sites that have experienced more severe disturbance that left exposed mineral soil are often dominated by *P. virginiana*. Shrub cover is typically sparse to moderate. Herbaceous cover is also sparse to moderate and of mixed species composition with no clear dominant. On sites dominated by *P. virginiana*, the understory is typically open with little shrub or herbaceous cover. Because this forest type is successional, most species that currently dominate the stand will decrease in dominance with stand development and succession. Many stands of this forest type were originally montane alluvial or cove forest and with time may redevelop the species composition and structure associated with these forest types.

The Tremont ATBI plot is located in this general forest type. Because of its heavy dominance by *L. tulipifera* and history of corporate logging, this site is classified as *Liriodendron tulipifera-Acer rubrum-Robinia pseudoacacia* Forest (Early Successional Appalachian Hardwood Forest; White et al. 2003). Although this site was heavily logged prior to creation of the Park (Fig. 1), its soil was the most productive of any of the ATBI plots and had the highest pH (5.7), CEC (12.3), and calcium saturation (62.1%) of all the plots (Table 3). In addition, its magnesium saturation (9.0%) was second only to the Cades Cove plot. The productivity and topographic position of this site suggest that it was a cove forest prior to logging. This secondary forest site contained a volume of DDW (126.1 m^3 ha^{-1}) comparable to some primary forests (Table 1).

Cove forests

NatureServe lists five different associations of cove forest in GSMNP, comprised of 2 acid cove and 3 cove hardwood associations (White et al. 2003), which are separated by the relative dominance of hardwoods versus *T. canadensis* and the richness of the herb layer. Cove forests are typically found in sheltered landscape positions below 1200 m, although some types are found above 1300 m. Aspects are generally northerly, but cove forests occur across a range of aspects. Rich coves, defined as Southern Appalachian Cove Forest (Rich Montane Type) by White et al. (2003), typically have canopies dominated by *Acer saccharum* Marsh. (sugar maple), *Aesculus flava* Ait. (yellow buckeye), *Tilia americana* L. (American basswood), and *Halesia tetraptera* var. *monticola* (Rehd.) Reveal & Seldi (silverbell). The shrub layer is typically sparse or absent, and the herbaceous layer is lush and species-rich. Although similar in composition, typic coves, defined as Southern Appalachian Cove Forest (Typic Montane Type) by White et al. (2003), contain a larger component of overstory *L. tulipifera* intermixed with *H. tetraptera*, *T. americana*, and *A. rubrum*. The shrub layer is sparse to moderate in cover, and the herb layer is diverse, but has lower cover than rich coves. Rich and typic cove forests cover approximately 25,000 ha of GSMNP (12% of total Park area; Table 2).

The canopies of acid cove forests are typically dominated by *T. canadensis*. White et al. (2003) delineated two types of acid cove forest: Southern Appalachian Acid Cove Forest (Typic Type) and Southern Appalachian Acid Cove Forest (Silverbell Type). The canopy of the typic type is dominated by *T. canadensis* and may also contain *L. tulipifera*, *B. lenta*, and *A. rubrum*. The shrub layer is typically dominated by *R. maximum*, which ranges in density from scattered to heavy. The herbaceous layer is typically sparse with low species richness. The typic type often occurs in association with upland streams. The Silverbell Type is typically dominated by *T. canadensis* and *H. tetraptera* var. *monticola*. Some forests of the Silverbell Type have dense *R. maximum* in the shrub layer, but typically the shrub layer is relatively open. The herbaceous layer of this type is typically sparse to moderate in coverage and usually contains more species than the typic type. Acid cove forests cover approximately 8900 ha in GSMNP (4% of total Park area; Table 2).

Five of the ATBI plots are located in cove forests: Albright Grove, Snake Den Ridge, Goshen Prong, Twin Creeks, and Purchase Knob (Fig. 1). Two of these plots—Albright Grove and Snake Den Ridge—are located in primary forest. The three other plots—Goshen Prong, Twin Creeks, and Purchase Knob—are located in secondary forest that regenerated following logging.

The Albright Grove ATBI plot is located in *Tsuga canadensis-Halesia tetraptera-(Fagus grandifolia, Magnolia fraseri)/Rhododendron maximum/Dryopteris intermedia* Forest (White et al. 2003). As described above, the common community name for this association is Southern Appalachian Acid Cove Forest (Silverbell Type). The canopy on this plot is dominated by *T. canadensis* and *H. tetraptera* var. *monticola* with a lesser component of *B. lenta* (Fig. 2). The shrub layer of this plot is fairly open with scattered *H. tetraptera* var. *monticola* and *A. saccharum* saplings and widely spaced stems of *R. maximum*. Percent herbaceous cover is moderate, and 34 herbaceous species have been identified on the plot. Structurally, Albright Grove is in the old-growth stage of stand development (Oliver and Larson 1996). Consequently, it contains the greatest live basal area of any plot sampled (Fig. 2), as well as a large volume of

DDW (164.4 m^3 ha^{-1}) and basal area of standing deadwood (SDW; 9.6 m^2 ha^{-1}; Table 1).

The Snake Den Ridge ATBI plot is also located in *Tsuga canadensis-Halesia tetraptera-(Fagus grandifolia, Magnolia fraseri)/Rhododendron maximum/Dryopteris intermedia* Forest (White et al. 2003). Although similar to Albright Grove in overstory composition, this site contains a more diverse canopy, including a fairly large component of *F. grandifolia* (Fig. 2). Compared to Albright Grove, this plot has a denser shrub layer dominated by *R. maximum.* In addition, the herbaceous layer is sparse and less diverse than Albright Grove (19 total herbaceous species). This site also is in the old-growth stage of stand development and contains the second highest basal area of any plot. This site also contains a volume of DDW comparable to other old-growth plots (134.8 m^3 ha^{-1}; Table 1).

The Goshen Prong ATBI plot is located in *Liriodendron tulipifera-Aesculus flava-(Fraxinus americana, Tilia americana* var. *heterophylla)/Actaea racemosa-Laportea canadensis* Forest (White et al. 2003). As described above, the common community name for this association is Southern Appalachian Cove Forest (Typic Montane Type). The overstory of this plot is dominated by *L. tulipifera*, with large components of *H. tetraptera* var. *monticola*, *Aesculus flava*, and *B. alleghaniensis* (Fig. 2). The shrub layer is very sparse, but the herb layer is species rich (52 herbaceous species). As with many post-logging forests that are still in the stem-exclusion stage of stand development (Oliver and Larson 1996), the plot contains relatively little coarse woody debris. Although this plot had a low pH compared to other low-to-mid-elevation secondary forests, its CEC and cation-saturation values were comparable to other coves (Table 3).

The Twin Creeks ATBI plot is also located in *Liriodendron tulipifera-Aesculus flava-(Fraxinus americana, Tilia americana* var. *heterophylla)/Actaea racemosa-Laportea canadensis* Forest. Its overstory is dominated by *L. tulipifera*, with large components of *A. rubrum* and *B. lenta* (Fig. 2). The shrub layer is dominated by *T. canadensis*, *R. maximum,* and *B. lenta*. However, prior to the onset of dogwood anthracnose, *C. florida* was a common understory species. The herbaceous layer of the plot is relatively species rich (34 herbaceous species), but no single species dominates cover. The soil chemistry of this site is very similar to other low-to-mid-elevation hardwood forests (Table 3).

The Purchase Knob ATBI plot is also located in *Liriodendron tulipifera-Aesculus flava-(Fraxinus americana, Tilia americana var. heterophylla)/Actaea racemosa-Laportea canadensis* Forest. However, the large component of *R. pseudoacacia* (Fig. 2) suggests that this site was logged more recently than the other secondary cove forests. This plot is located at a higher elevation, by far, than any other cove forest ATBI plot (1324 m). Northern hardwood forests typically occur at this elevation, but because this plots contains *L. tulipifera* as a canopy co-dominant, it is not classified as a northern hardwood forest (White et al. 2003). The understory of this plot is open and dominated by *A. saccharum*, *H. tetraptera* var. *monticola*, and *T. canadensis*. The herbaceous layer contains more species than any other cove forest (63 herbaceous species). Perhaps as a result of slower decomposition at higher elevations, this plot has the highest organic matter content of any low-to-mid-elevation secondary forest (Table 3).

Hemlock forests

NatureServe (White et al. 2003) has delineated two associations of hemlock forest in GSMNP: Southern Appalachian Eastern Hemlock Forest (White Pine Type) and Southern Appalachian Eastern Hemlock Forest (Typic Type). Although *T. canadensis* occurs in the overstory of both types, the canopy of the white pine type is dominated or co-dominated by *P. strobus*. The shrub layer of these forests is typically dominated by *R. maximum* and *L. fontanesiana*. The herb layer is sparse; typical species include *Dryopteris intermedia* (Muhl. Ex illd.) Gray (intermediate wood fern), *Goodyera pubescens* (Willd.) R. Br. Ex Ait. F. (downy rattlesnake-plantain), *Mitchella repens* L. (partridgeberry), and *Polystichum acrostichoides* (Michx.) Schott (Christmas fern). These forests typically occur on lower protected slopes and terraces below 2300 m elevation. According to Madden et al. (2004), hemlock forest comprise only 2% of the Park's forest cover (Table 2). However, *T. canadensis* is one of the most common tree species in the Park and occurs as a co-dominant or subcanopy species across a broad range of forest community associations.

Montane oak-hickory forests

NatureServe has identified eight associations of montane oak-hickory forests in GSMNP (White et al. 2003). These forests occur across a wide range of elevations extending from 340 m to 1370 m and are found on a range of aspects. Generally, these forests occur on more-exposed convex-shaped slopes than cove forests. However, this forest type is often found in protected landscape positions. Montane oak-hickory forest is the most common general forest type in GSMNP and covers approximately 64,600 ha (31% of total Park area; Table 2). The Cataloochee ATBI plot is located in this general forest type.

The Cataloochee ATBI plot is located in *Quercus rubra-Acer rubrum/Calycanthus floridus-Pyrularia pubera/Thelypteris noveboracensis* Forest (White et al. 2003). The common community name for this association is Appalachian Montane Oak-Hickory Forest (Red Oak Type). The overstory of this plot is dominated by *Quercus rubra* L. (northern red oak) with lesser amounts of *A. rubrum*, *Quercus prinus* L. (chestnut oak), and *Quercus alba* L. (white oak; Fig. 2). The shrub layer of this plot is relatively open and dominated by *Acer pensylvanicum* L. (striped maple), *Amelanchier laevis* Wieg. (serviceberry), and sprouts of *C. dentata*. The herbaceous layer of this plot contained 51 species.

Although this stand has old-growth characteristics, its total basal area is comparable to that of the low-to-mid-elevation secondary forest ATBI plots (Fig. 2). However, the DDW volume (Table 2) of this plot is higher than that of other old-growth plots (Albright Grove, Snake Den Ridge, and Ramsay Cascade). Much of the DDW on this plot was *C. dentata* that was killed by chestnut blight at the turn of the century, suggesting that this forest was once heavily dominated by *C. dentata*. The lower basal area found on this site suggests that this stand is still accruing biomass following the loss of *C. dentata*. The very low basal area of SDW (1.5 $m^2 ha^{-1}$; Table 1) suggests that the dominant *Quercus* overstory has not begun to experience significant mortality.

Xeric ridge forests

This suite of forest types is dominated by *Pinus* and *Quercus* species and typically occurs on ridges and exposed south- to west-facing slopes. This broad group of forest types covers 33,330 ha of GSMNP (16% of total Park area, Table 2). NatureServe has identified 7 associations within the general forest type that occur within the Park and two that are likely to occur. The more xeric of these types are dominated by yellow pine species: *Pinus echinata* P. Mill. (shortleaf pine), *Pinus pungens* Lamb. (Table Mountain pine), *Pinus rigida* P. Mill. (pitch pine), and *P. virginiana*. *Pinus pungens*, which is a dominant species in the *Pinus pungens-Pinus rigida*-(*Quercus prinus*)/*Kalmia latifolia-Vaccinium pallidum* Forest association (White et al. 2003), is endemic to the central and southern Appalachian Mountains. This species has serotinous cones and is likely dependent upon fire for reproduction (Zobel 1969, but see Barden 2000). Over the past 20 years, yellow pine stands throughout the southern Appalachians have been decimated by the southern pine beetle (SPB). Although this insect is native, over 70 years of fire suppression have altered its role in the disturbance regime of native pine forests (Harrod et al. 1998). As a result of fire suppression, overstory tree density and the density of *Kalmia latifolia* L. (mountain laurel) have increased and thick layers of leaf litter have accumulated. The resulting heavy shade and thick duff layer prevent pine seedlings from establishing (Welch et al. 2000). The increased density of pine trees increases the abundance and spread of the SPB, resulting in greater rates of mortality (Zhang and Zeide 1999). Following mortality, the lack of pine regeneration causes the developing stand to be dominated by hardwood species.

Less xeric associations within this general type include forests dominated by *P. strobus*, *Q. prinus*, *Quercus coccinea* Muenchh. (scarlet oak), and *Q. alba*. These forest types are typically found on lower ridges and less-exposed slopes. This general forest type also includes an association comprised of *Q. prinus* and *Q. coccinea*, but without a yellow pine component. The Ramsay Cascade ATBI plot is located in this association.

The Ramsay Cascade ATBI plot is located in *Quercus (prinus, coccinea)/ Kalmia latifolia/ (Galax urceolata, Gaultheria procumbens)* Forest (White et al. 2003). The common community name for this association is Chestnut Oak Forest (Xeric Ridge Type). *Quercus prinus* dominates the overstory (Fig. 2) and occurs over a dense shrub layer of *R. maximum*, *K. latifolia*, and

Gaylussacia ursina (M.A. Curtis) Torr. & Gray ex Gray (bear huckleberry). The herbaceous layer is dominated by typical dry-site species such as *G. urceolata* and *Smilax rotundifolia* L. (greenbrier). Overall, the herbaceous layer is relatively depauperate of species (11 herbaceous species). This plot contained the lowest volume of DDW of any low-to-mid-elevation primary forest sampled (74.0 m^3 ha^{-1}; Table 1). Soils were acidic (pH = 4.0) with low CEC and cation saturation (Table 3).

High-elevation hardwood forests

This group of forest types includes northern hardwood forests, high-elevation oak forests, forested boulderfields, and beech gap forests. These forests cover 34,109 ha of GSMNP (17% of total Park area; Table 2). NatureServe identifies 11 associations within this class of forest types. These forest types all occur at elevations greater than 1040 m and range as high as 1645 m. More-exposed landforms with more southerly aspects are often dominated by *Q. rubra* or *Q. alba*. Less-exposed sites with more northerly aspects are often dominated by northern hardwood species including *Betula alleghaniensis* Britt. (yellow birch), *A. saccharum*, *Aesculus flava*, and *F. grandifolia*. In northeastern North America, large-scale decline of *A. saccharum* has occurred, likely as a result of the combined effects of insect defoliation, soil acidification, and drought (Horsley et al. 2002). An exotic insect, *Taeniothrips inconsequens* (Uzel; pear thrips), that has been a major contributor to *A. saccharum* decline in the Northeast was recently collected in GSMNP by an ATBI researcher. High-elevation forests in the Park have long experienced heavy levels of acid deposition (Shaver et al. 1994), and drought is a common occurrence in the southern Appalachians (Clinton et al. 2003). Therefore, this forest type should be monitored for the onset of *A. saccharum* defoliation and decline.

This class of forest types also includes one of the most threatened communities in the southern Appalachians: beech gap forests. These forests occur at elevations above 1370 m and typically are located on upper slopes or in saddles or gaps. They often are found within a matrix of other high-elevation hardwood forests, but also occur as islands within *P. rubens* forest. These unique forests are comprised of nearly pure stands of *F. grandifolia* where reproduction is almost exclusively from root sprouts (Russell 1953). This results in high stem densities of *F. grandifolia*, but also produces low genetic diversity within the species (Kitamura et al. 2001, but see Morris et al. 2004).

Beech forests throughout eastern North America have been decimated by beech bark disease, an exotic insect-fungal pathogen complex (Houston 1994). Infection with beech bark disease is initiated with an infestation of *Cryptococcus fagisuga* Lind. (beech scale), a parthenogenic insect that facilitates infection of meristematic tissue with one of two species of *Nectria* fungi: *N. coccinea*, an exotic species, or *N. galligena*, a native species (Mahoney et al. 1999). Between 1986–2002, Vandermast (2005) found an annual mortality rate of 5.4% in infected stands and nearly 100% cumulative mortality in the most severely infected stands.

Three ATBI plots are located in beech gap forests (Indian Gap, Trillium Gap, and Double Springs Gap). All of these plots are in *Fagus grandifolia/ Carex pensylvanica–Carex brunnescens* Forest (White et al. 2003). The canopies of all three plots are dominated by *F. grandifolia*, although all three stands have experienced heavy dieback and mortality from beech bark disease (Fig. 2). The canopy at Trillium Gap has a large component of *H. tetraptera* var. *monticola*, and the canopy at Double Springs Gap has a large component of *Aesculus flava*. The shrub layers of all three plots are heavily dominated by root sprouts of *F. grandifolia*. *Carex pensylvanica* Lam. (Pennsylvania sedge), *D. intermedia*, *Rugelia nudicaulis* Shuttlw. Ex Chapman (Rugel's ragwort), and *Laportea canadensis* (L.) Weddell (wood-nettle) are important herbaceous species at Trillium Gap and Indian Gap. The herbaceous layer of Double Springs Gap was dominated by *C. pensylvanica* and two fern species: *D. intermedia* and *Athyrium filix-femina* (southern lady fern). Total herbaceous-layer richness was similar at the three sites; Indian Gap contained 27 herbaceous species, Trillium Gap contained 23 species, and Double Springs Gap contained 20 species. Soils at all three beech gap plots were very acidic (maximum pH = 3.5) with low to moderate cation saturation and CEC (Table 3).

Spruce-fir forests

Spruce-fir forests cover 15,500 ha of GSMNP (8% of total Park area; Table 1). *Picea rubens* and *A. fraseri* are the dominant overstory species, with *A. fraseri* typically dominating stands above 1890 m elevation, *P. rubens* co-dominating between approximately 1675 and 1890 m elevation (Whittaker 1956), and *P. rubens* co-dominating with northern hardwoods and *T. canadensis* as low as 1480 m elevation. Although the range of *P. rubens* extends to northeastern Canada, *A. fraseri* is endemic to the southern Appalachian Mountains (White 1984). *Betula alleghaniensis* is the most common hardwood species in spruce-fir forest, with *Acer spicatum* Lam. (mountain maple), *Prunus pensylvanica* L. f. (pin cherry), and *Sorbus americana* Marsh. (American mountain ash) also occurring (Whittaker 1956). NatureServe identified 8 associations of spruce-fir forest in GSMNP (White et al. 2003, Table 2).

Because of their topographic and geographic isolation, spruce-fir forests of the southern Appalachian Mountains are rich in rare and endemic species. Eight plant species, 17% of the characteristic species of these forests, are endemic to the high peaks of the southern Appalachians (White 1984). One of these species, *R. nudicaulis*, is only found within the boundary of Great Smoky Mountains National Park. Southern Appalachian spruce-fir forest is also listed as critical habitat for the federally endangered *Microhexura montivaga* Crosby & Bishop (spruce-fir moss spider) and provides important foraging habitat for two federally endangered southern Appalachian subspecies of northern flying squirrel (*Glaucomys sabrinus fuscus* Miller and *G. s. coloratus* Handley; Loeb et al. 2000).

Spruce-fir forests in the southern Appalachians were commercially logged, and huge slash fires occurred after logging. As a result, present-day southern Appalachian spruce-fir forest has been estimated to occupy 10% to 50% of its former extent (Korstian 1937, Saunders 1979). The reduction of spruce-fir forest in GSMNP has been less severe than elsewhere in the southern Appalachians. According to Pyle (1988), the area that became GSMNP contained 17,910 ha of spruce-fir forest prior to logging. Following logging, this total was reduced by 25% to 13,370 ha. Dull et al. (1988) estimated that present-day spruce-fir forest in the southern Appalachians occupies 26,610 ha, of which 74% is found in the Great Smoky Mountains. According to the vegetation map developed by Madden et al. (2004), GSMNP contains 15,514 ha of spruce-fir forest.

Over the past 40 years, spruce-fir forests have been decimated by *Adelges piceae* (Ratzenburg) (balsam woolly adelgid), an aphid-like insect introduced from Europe that attacks *A. fraseri*. The adelgid feeds in the bark fissures of *A. fraseri* trees over 4 cm dbh (Eagar 1984), causing the tree to produce abnormally short and heavily lignified tracheids which reduces water conduction and kills the tree in 2–7 years (Amman and Speers 1965). Across the southern Appalachians, most mature *A. fraseri* trees have died as a result of adelgid infestation (Jenkins 2003, Pauley and Clebsch 1990). Because they occur at high elevations in exposed topographic conditions, these forests also receive the highest levels of acid deposition and ozone exposure in GSMNP (Johnson et al. 1991, Shaver et al. 1994).

Three of the ATBI plots are located in spruce-fir forest: Clingmans Dome, Mt. LeConte-Boulevard, and Mt. Leconte-West Point. The three plots are located in *Abies fraseri/Viburnum lantanoides/Dryopteris campyloptera–Oxalis montana/Hylocomium splendens* Forest (White et al. 2003). The common community name for this association is Fraser Fir Forest (Deciduous Shrub Type). As a result of heavy overstory mortality from the balsam woolly adelgid, all three of these plots have relatively low basal area of living trees. This is particularly evident in the two plots located on Mt. LeConte. Most of the overstory trees (≥10 cm dbh) are *P. rubens* or species other than *A. fraseri* (Fig. 2). Due to heavy mortality of *A. fraseri*, these plots have large volumes of DDW and basal area of SDW (Table 2). Post-adelgid regeneration of *A. fraseri* dominated the sapling layer of two plots: Clingmans Dome and Mt. LeConte-Boulevard (65% and 82% of total sapling density, respectively). Although *A. fraseri* is present, saplings in the Mt. LeConte-West Point plot consist largely of hardwood species, with *Viburnum lantanoides* Michx. (hobblebush) comprising over 90% of the total density of saplings. The shrub layers at both Mt. LeConte plots contain heavy coverage of *Rubus canadensis* L. (smooth blackberry), an early-successional species that often dominates spruce-fir understories following *A. fraseri* mortality. Soils on the three plots are acidic with low to moderate cation saturation (Table 3).

Non-forested Communities

Although most of GSMNP is forested, the Park does contain some notable non-forested community types. Because they are surrounded by forest, these communities may serve as islands of habitat for species that require open non-forested or forest-edge habitat. In GSMNP, heath balds, grassy balds, and pastures/old fields are the three most common non-forested community types (Madden et al. 2004).

Heath balds

Heath balds are an unusual shrubland community type whose origin has long been a mystery to ecologists. NatureServe has identified 2 associations of heath balds in GSMNP (White et al. 2003). They occur at elevations above 1270 m on exposed ridges, steep slopes, and rock outcrops and cover approximately 2600 ha (approximately 1% of total Park area; Table 2). The vegetation of heath balds consists of dense, nearly impenetrable ericaceous shrubs. *Rhododendron catawbiense* Michx. (catawba rhododendron) is typically the dominant species, but *R. maximum* and *K. latifolia* are also common. Because of their thick shrub cover, heath balds are very resistant to tree invasion and have not changed in area within GSMNP since the 1930s (White et al. 2001). Other less common species include *Leiophyllum buxifolium* (Berg.) Ell. (sand myrtle) and *Rhododendron carolinianum* Rehd. (Carolina rhododendron). Typically, herbaceous cover is sparse and consists of few species. The presence of heath balds is positively correlated with burned sites, old-growth conditions, and a highly acidic rock type. An ongoing study of bald age and formation has revealed radiocarbon ages of base organic deposits ranging from approximately 1000 to 3000 years before present (Robert Young, Western Carolina University, Cullowhee, NC, pers. comm.). These dates represent a minimum age of formation for each bald. In addition, the base of the soil has consistently been a thick, persistent charcoal layer, suggesting that bald formation may be initiated by fire. However, the carbon dating results show that these fires predate European settlement.

One ATBI plot, Brushy Mountain, is located in a heath bald. This site is classified as *Kalmia latifolia–Rhododendron catawbiense–(Gaylussacia baccata, Pieris floribunda, Vaccinium corymbosum* Shrubland (common community name: Southern Appalachian Mountain Laurel Bald; White et al. 2003). Soils on this site were very acidic (pH = 3.7) with low cation saturation (Table 3). Because of the slow decomposition of ericaceous litter, this plot had the highest percent organic matter of any plot (4.4%). The influence of this organic matter on soil exchange sites contributed to the moderate CEC value of this site (CEC = 8.3).

Grassy balds

As the name describes, grassy balds are treeless areas covered by grasses, sedges, and forbs. In GSMNP, they occur on gently sloping ridges between

1320 m and 1615 m elevation. *Danthonia compressa* Austin ex Peck (mountain oat grass) strongly dominates vegetation. Other characteristic species include *Potentilla canadensis* L. (dwarf cinquefoil), *Rumex acetosella* L. (common sheep sorrel), and *Cinna latifolia* Griseb. (woodreed). Some balds contain populations of unusual or rare plants that cannot grow in shady environments. Although most balds in GSMNP are thought to have originated from livestock grazing, two balds—Gregory Bald and Parsons Bald—are described as "bald spots" in an 1821 survey of the Tennessee–North Carolina state line (Langdon 1999).

Following the creation of the Park and the resulting cessation of grazing, trees and shrubs began to encroach onto the balds. Early experiments revealed that burning accelerated the advancement of woody species by stimulating sprouting from the root collar of burned trees (Langdon 1999). Grazing or repeated cutting are the most effective techniques to control the invasion of woody species. Currently, the National Park Service uses mechanical cutting of woody stems to manage two balds in GSMNP, Gregory and Andrews Balds, both of which contain ATBI plots. Soils on these plots had moderate pH, low CEC, and low cation saturation (Table 3).

Pasture and old fields

Great Smoky Mountains National Park contains approximately 940 ha of pastures, old fields, and other graminoid-dominated areas (including grassy balds) comprised of 2 associations (Table 2). Most pastures and old fields are located within Cades Cove, Oconaluftee, and Cataloochee and are maintained as cultural landscapes. Many of these areas, including Cades Cove, were planted in *Lolium pratense* (Huds.) S.J. Darbyshire (meadow fescue) after creation of GSMNP. However, composition is variable and some areas are dominated by other species including *Andropogon glomeratus* (Walt.) B.S.P. (marsh broomsedge) and numerous forb species. The National Park Service has an ongoing program to restore native grasses in some parts of Cades Cove through the combined use of prescribed fire, herbicide, and planting. An ATBI plot is located within an old-field in Cades Cove. This site has a mixed composition of old-field and grassland species and includes a marshy area adjacent to a historically disturbed stream. The soils at this site had a relatively high pH (pH = 5.7), CEC (8.8), and cation saturation (48.4/2.7/10.9; Ca/K/Mg) (Table 3).

Rare and unusual communities

Great Smoky Mountains National Park contains numerous small, spatially scattered community types that may provide habitat for rare or unusual species. These communities include dry cliffs and outcrops, spray cliffs associated with waterfalls, rocky summits, bogs, marshes, and seeps. Many of the rare, threatened, and endangered species that occur in the Park are found in these habitats. Although a discussion of these communities is beyond the scope of this paper, White et al. (2003) provides detailed descriptions.

Conclusions

The wide variety of vegetation communities in GSMNP is not only a testament to the vascular plant diversity of southern Appalachia, but also provides habitat for and depends upon a wide range of other less-studied taxa. When describing the Great Smoky Mountains in 1913, Horace Kephart (Kephart 1976) stated that "upon them today the last great hardwood forests of our country stand in primeval majesty, mutely awaiting their imminent doom." Although the creation of GSMNP in 1934 prevented their complete loss, over the past 70 years, these forests have been severely impacted by a staggering array of factors. Exotic insects and disease have fundamentally altered ecological relationships and in many cases effectively eliminated entire species. Control of exotic insects, diseases, plants, and vertebrates requires continuous effort. Abiotic factors, such as acid deposition and altered disturbance regimes, have also contributed to the degradation of many communities. Understanding the impacts of both biotic and abiotic factors is critical to the successful management of this biologically rich and wondrous place. The information produced by the ATBI will take us one step closer to truly understanding and preserving the biodiversity of GSMNP.

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