

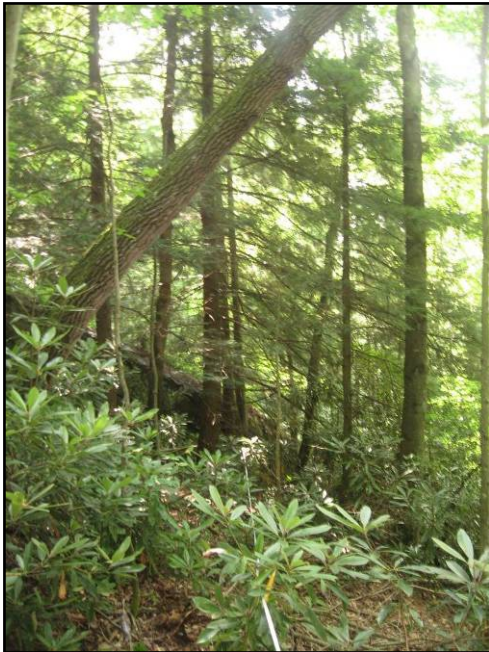
National Park Service
U.S. Department of the Interior

Northeast Region
Philadelphia, Pennsylvania



Hemlock Ecosystem Monitoring of New River Gorge National River and Gauley River National Recreation Area Vegetation and Bird Communities: 1998–2008

Natural Resources Report NPS/NER/NRR—2009/019



ON THE COVER

Top Left: Tape stretched along a sampling transect in a mesic hemlock sampling plot; photo by Jason Liddle.

Top Right: Hemlock woolly adelgid (*Adelges tsugae*) on eastern hemlock (*Tsuga canadensis*); photo by John Perez.

Bottom Right: Plot corner of a xeric hemlock sampling plot; photo by Jason Liddle.

Bottom Left: Adult female wood thrush (*Hylocichla mustelina*); photo by Matt Shumar.

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Natural Resources Report NPS/NER/NRR—2009/019

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U.S. Department of the Interior
National Park Service
Northeast Region
Philadelphia, Pennsylvania

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Abstract

We initiated a long-term hemlock ecosystem monitoring study in 1998 on the New River Gorge National River (NERI) and Gauley River National Recreation Area (GARI), in Nicholas, Fayette, and Raleigh counties, West Virginia, to quantify the effects of hemlock woolly adelgid (HWA) on forest ecosystem dynamics. Hemlock vigor and degree of adelgid infestation were sampled in each fall 1998 through 2007 except 1999 and 2005; vegetation structure and composition were sampled in summer 1999 and 2007; and avian populations were sampled each summer 1999 through 2008. HWA was first detected on sampling plots in 2004 when it was found on eight of 36 plots and reached a high of 22 plots in 2006. Although hemlock crown vigor has declined, limited hemlock mortality has occurred. Consequently, vegetation structure and bird communities have changed little. However, because the literature suggests that tree mortality can occur within four to six years of infestation, we expect hemlock mortality to ensue.

Keywords: adelgids, vegetation structure composition, songbirds.

Introduction

Introduced forest pests such as the hemlock woolly adelgid (*Adelges tsugae*; HWA) can substantially change native forest ecosystems and the wildlife communities they support. The HWA, introduced in Virginia in the early 1950s (Stoetzel 2002), is a serious pest of eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*T. caroliniana*) causing extensive hemlock mortality (Souto et al. 1996). The HWA was first detected near our study areas in West Virginia on the Bluestone River in April 2000 and the New River Gorge National River in March 2002 (New River Gorge National River, J. Perez, Biologist, pers. comm., 2/2007). Hemlock trees occur throughout these areas and the Gauley River National Recreation Area in moist coves, along stream and river corridors, and in mixed conifer/deciduous forests on rock outcrops at the rim of gorges. Mortality of hemlocks could substantially change the appearance and composition of plant communities in these areas.

Hemlock ecosystems also harbor avian species dependent on conifer habitats (Tingley et al. 2002). After infestation by adelgids and as the plant community changes from primarily hemlock dominated to hardwood dominated (Orwig and Foster 1998), one would expect the avian community to change. To document avian population changes in the hemlock community in response to HWA infestation, it is necessary to identify species richness and abundance of the avian community prior to adelgid arrival and during initial infestation before substantial changes occur in the hemlock vegetative community. Demographics of avian species are often tied to aspects of the plant community such as vertical structure, density, and relative abundance of species (Franzreb 1983); thus, vegetative structural changes can result in changes in the avian community (Litwin and Smith 1992; McDermott and Wood 2009).

Prior to adelgid infestation, we established a long-term hemlock ecosystem monitoring study on the New River Gorge National River (NERI) and Gauley River National Recreation Area (GARI). The study was initiated in 1998 with baseline surveys of adelgid presence and hemlock vigor in fall 1998. In summer 1999, baseline vegetation composition and structure were quantified (Wood 1999a, 1999b) and baseline songbird surveys were initiated (Wood 2004). The study was designed to measure change across the broad landscape represented by NERI and GARI, covering an extensive area spanning approximately 97 km (60 mi) from north to south (Figure 1) and ranging in elevation from 427–853 m (1,401–2,799 ft). Our pre-infestation data on the NERI/GARI hemlock forests provide a rare dataset of the extant Appalachian hemlock ecosystem prior to the arrival of the HWA.

The overall objectives of our long-term study are to (1) document HWA invasion and the resulting hemlock decline and mortality, (2) quantify any changes in plant species composition, structure, abundance, and richness over time, and (3) quantify avian richness and abundance to relate these songbird metrics to structural changes in vegetation characteristics in a variety of hemlock habitats within NERI and GARI. Vegetation sampling was designed to measure changes in species composition in all structural layers of the plant community using an array of sampling techniques to quantify: 1) density and species richness of trees, saplings, shrubs, and vines; 2) vertical and horizontal cover of all vascular plants; 3) frequency of occurrence of

understory vascular plants; 4) hemlock tree health, morbidity, and mortality by measuring diameter, live crown ratio, vigor, and straightness; and 5) diameter of all other tree species. As HWA invasion is just beginning to occur on our study plots, this report summarizes data from pre-invasion and during initial HWA outbreaks.

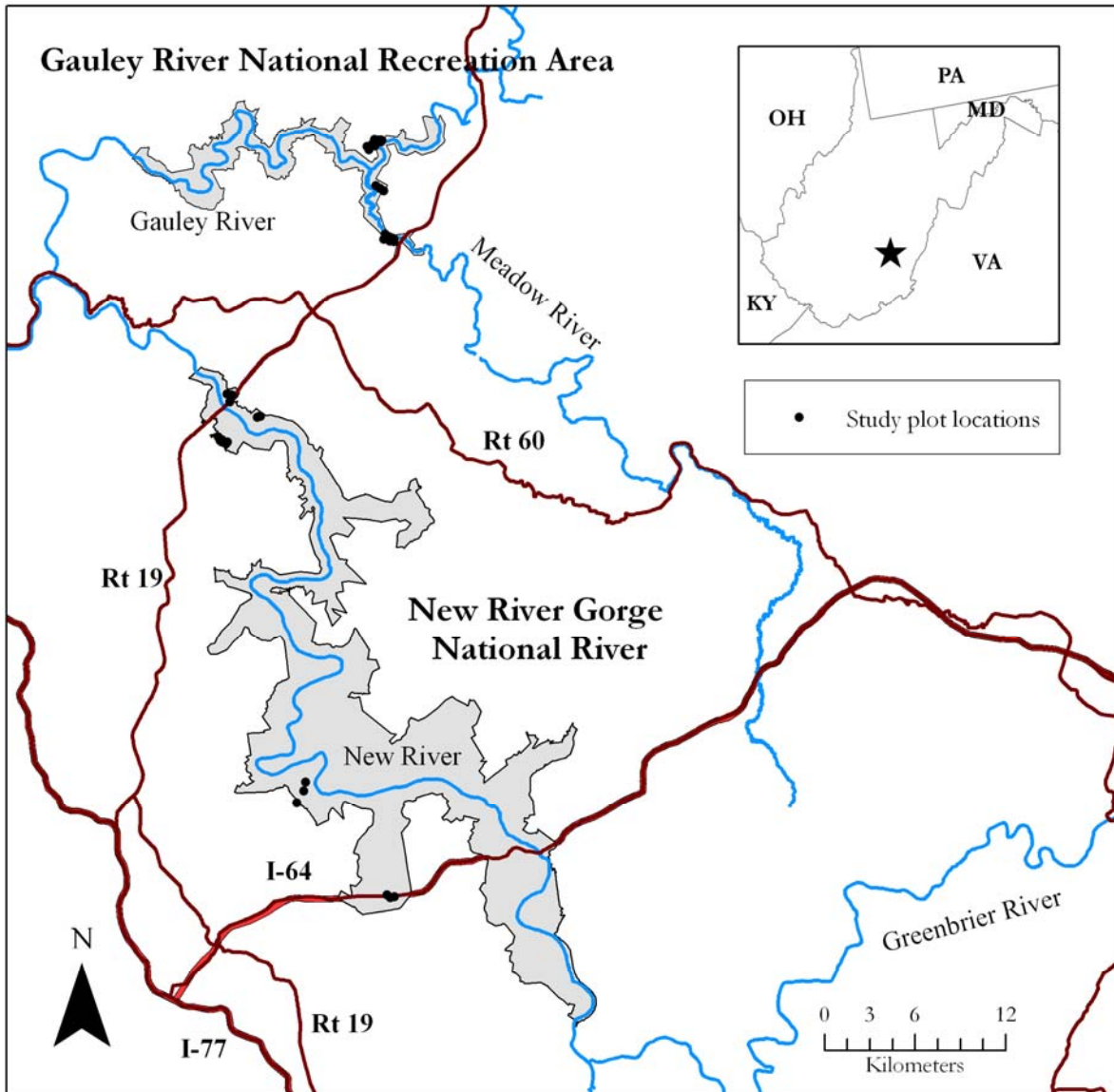


Figure 1. Locations of the 36 hemlock study plots at Gauley River National Recreation Area and New River Gorge National River, West Virginia.

Study Area and Methods

We established long-term hemlock ecosystem monitoring plots in the New River Gorge National River (NERI) and Gauley River National Recreation Area (GARI), in Nicholas, Fayette, and Raleigh counties, West Virginia, during November 1998 (Wood 1999a, 1999b). National Park Service (NPS) staff directed that the plots would sample a variety of habitats throughout the parks with the intention of gathering the maximum amount of data on biodiversity, and that plots be relatively easily accessible for subsequent monitoring (i.e. no more than 1.6 km (1 mi) from a road or trail head). Because accurate vegetation maps of NERI and GARI were not available at the time the study was initiated, candidate hemlock stands initially were identified by recommendations from NPS resource management staff familiar with the two areas. After field reconnaissance of these sites, 36 plots with three classes of soil moisture availability (see below) were non-randomly placed in hemlock stands. NPS staff identified specific areas of the parks where plots would be placed (Table 1) because these areas had significant amounts of hemlock present and were of particular interest. The remaining plots were placed in areas of hemlocks that would meet the distribution, accessibility, and soil moisture criteria described above. We sampled 36 plots to accommodate the large area NPS wanted to include in the study, yet make it logistically possible to sample such widely separated plots given time and funding constraints. Study plots ranged from northern sites at Carnifex Ferry Battlefield State Park adjacent to a segment of the Gauley River within Gauley River National Recreation Area to the southern sites at Kate's Branch and Grandview units of the New River Gorge National River (Figure 1, Table 1). Detailed plot locations are available in Wood (1999a).

To logistically accommodate variability in soil moisture, elevation, slope and aspect, three soil moisture classes (hydric, mesic, and xeric) were defined (Wood 1999a). Hydric plots were placed in relatively moist, north-facing ravines or slopes along the Meadow, Gauley, and New rivers and in a perched wetland situated above the rim of New River Gorge along Fern Creek. Xeric plots were placed on relatively dry sites on western or southern aspects often just below the rim of gorges and on mid-slopes where an impermeable layer of rock was close to the soil surface; at these sites, small patches and narrow bands of hemlock trees occur where groundwater seeps out. Mesic plots were not north- or south-facing and generally were mid-slope rather than near the top or bottom of the gorges. Because suitable mesic sites could not be found in the northern area of NERI (New River North), six mesic plots were placed in the southern area (New River South) (Table 1). Thus, the three soil moisture classes were each replicated 12 times (Table 1).

Each vegetation plot was 400 m² (4,305 ft² [0.04 ha {0.1 ac}]) in size, with dimensions similar to other HWA stand-level monitoring studies (Mahan et al. 1998; Orwig and Foster 1998). Depending on site conditions, plots were placed either within a hemlock stand or within an isolated patch of hemlock trees, and were square (20×20 m [65.6×65.6 ft]) or rectangular (10×40 m [32.8×131.2 ft]) depending on the shape and size of the hemlock patch. Centers and corners of each plot were permanently marked. On sites where hemlock was a co-dominant rather than the dominant tree species, plot-centers were deliberately placed where there was a visible amount of hemlock canopy cover.

Table 1. Locations of 36 hemlock ecosystem monitoring plots at Gauley River National Recreation Area (NRA) and New River Gorge National River (NR), West Virginia.

Study Sites	Moisture Class			Total
	Hydric	Mesic	Xeric	
Gauley River NRA (Summersville Dam Quadrangle)				
Meadow River	3	3	3	9
Gauley River (Carnifex Ferry Battlefield State Park) ^a	3	3	3	9
New River Gorge NR North (Fayetteville Quadrangle)				
Fern Creek ^a	3	-	-	3
Burnwood/Ames Heights ^a	-	-	3	3
Wolf Creek	3	-	3	6
New River Gorge NR South (Prince Quadrangle)				
Kates Branch ^a	-	3	-	3
Grandview ^a	-	3	-	3
Total Plots	12	12	12	36

^aSites specified by NPS personnel for sampling. Remaining sites were placed in hemlock stands to meet criteria of dispersed across the parks, accessibility, and equal sample size in each moisture class.

To accommodate the avian study, plots were placed at least 250 m (820 ft) apart when possible. Eight pairs of plot centers were <250 m (820 ft) apart; none were <100 m (328 ft) apart. Generally, 250 m (820 ft) between point count stations is considered sufficient for independence between avian sampling stations (Ralph et al. 1993), although some studies have used distances of 100 m (328 ft) (Pendleton 1995). Although some large hemlock stands contained more than one plot, we considered the plot the sampling unit because plots met the above criteria for independence.

Hemlock Stand Age

Three hemlock trees (≥ 8 cm [3.15 in] diameter at breast height [dbh; measured 1.4 m (4.6 ft) above the ground]) from each plot (total 108) were cored with an increment borer in April 1999. Whenever possible, one core was taken approximately at breast height from a tree randomly selected from each of the three largest diameter classes present in each plot. Tree rings were counted, without staining, using a dissecting stereo-microscope. If the tree pith was missed in the coring process or if the radius of the tree was greater than the length of the borer, the total number of rings was estimated. This estimate took into account both the measured radius of the tree and the growth rate of any older trees cored at the same geographical location in the study area. Mean age of the three cored trees was used to represent stand age for the plot. Stand ages were compared among the three soil moisture classes using a fixed-effect model, nested analysis of variance (ANOVA) that included moisture class and the replicated plot variable as fixed effects and geographic location as a blocking factor.

Geographic location included the Gauley River and Meadow River (GARI) plots as one block and New River North and South (NERI) as a second block to account for geographic variation. However, because plot placement was not random, we considered geographic location (GARI vs. NERI), soil moisture class, and plot within location as fixed effects in statistical analyses.

Transect (four within each plot) and any sub-sampling on transects, were considered random effects.

Hemlock Diameter, Vigor, Live Crown, and HWA Infestation

We initiated baseline surveys of adelgid presence and hemlock tree vigor, live crown ratio, and diameter in fall 1998. These data were collected each year through fall 2007, except for 1999 and 2005. Data were collected to coincide with the November through April period in which the current season's HWA population typically exhibits woolly characteristics (Onken et al. 1994).

Diameter at breast height was measured and tallied for all live and standing dead hemlock trees that were rooted within or intersecting the outside perimeter of each 400 m² (4,305 ft²) plot. Trees were defined as ≥8 cm (3.15 in) dbh. Each tree was given a crown-vigor class rating which was an index of the health of the live crown based on Onken et al. (1994). The entire crown was inspected using binoculars and ranked as 1=>95% healthy crown, 2=>75–95%, 3=>50–75%, 4=>25–50%, or 5=0–25%. Additionally, a live crown ratio was visually estimated as the percentage of the total tree height with live foliage (Miller et al. 1998). For each tallied hemlock, the degree of HWA infestation was ranked from 1 to 4, with 1=heavily speckled and visible from 30 m (98 ft), 2=moderately speckled, 3=lightly speckled with only a few scattered specks, and 4=none. Data summaries presented in results are based only on live hemlock trees.

The distribution of live hemlock trees assigned to 10 dbh classes grouped by 10-cm (4-in) intervals (Figure 2) was compared between 1998 and 2007 with a Cochran-Mantel-Haenszel (CMH) chi-square statistic which allowed us to simultaneously test for differences among the three moisture classes. The CMH test also was used to compare the distribution of hemlock trees assigned to the four HWA ranks and to the five categories of live crown ratios in 1998 versus 2007 and among the three soil moisture classes.

Vegetation Sampling and Analyses

Vegetation structure and composition initially were sampled in summer 1999, and then re-sampled in summer 2007 using methods summarized in Wood 1999b and detailed in field sampling protocols (Wood 1999a). Personnel were trained in vegetation sampling protocols.

Stems of all live saplings (<8 cm [3.15 in] dbh and ≥1.4 m [4.6 ft] tall) and shrubs (woody plants ≥1.4 m [4.6 ft] tall) were counted and identified to species on four belt transects within each plot. Each transect was 2×10 m (6.56×32.8 ft) or 20 m² (215 ft²). Belt transects began 1 m (3.28 ft) from the plot center on 20×20 m (65.6×65.6 ft) plots (5 m [16.4 ft] on 10×40 m [32.8×131.2 ft] plots) and extended towards each plot corner. All live tree stems (those ≥8 cm [3.15 in] dbh) on the 400 m² (4,305 ft²) plot were tallied, identified to species, and dbh was measured and recorded. Stem density of shrubs, saplings, and trees and overall species richness were compared between the two years with a fixed-effect model, nested ANOVA. For species richness and tree stem density, the ANOVA model included variables for geographic location and soil moisture class. Sapling and shrub stem densities were combined for analyses and the ANOVA model included variables for geographic location, soil moisture class, plot replicate, and transect. As mentioned above, because plot placement was not random, we considered geographic location (GARI vs. NERI), soil moisture class, and plot within location as fixed

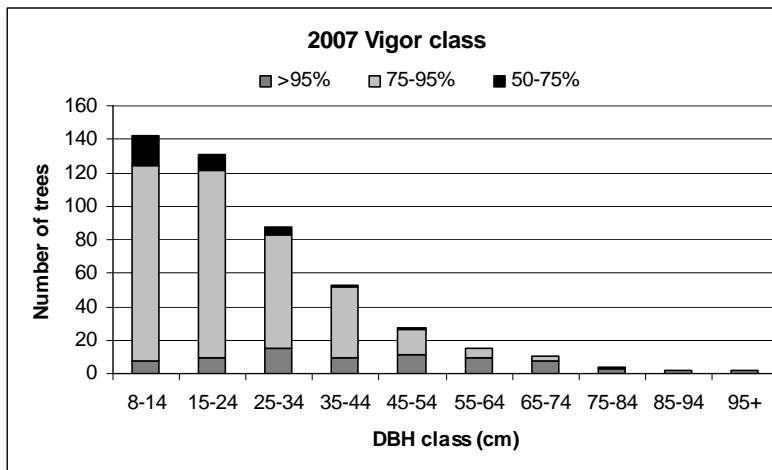
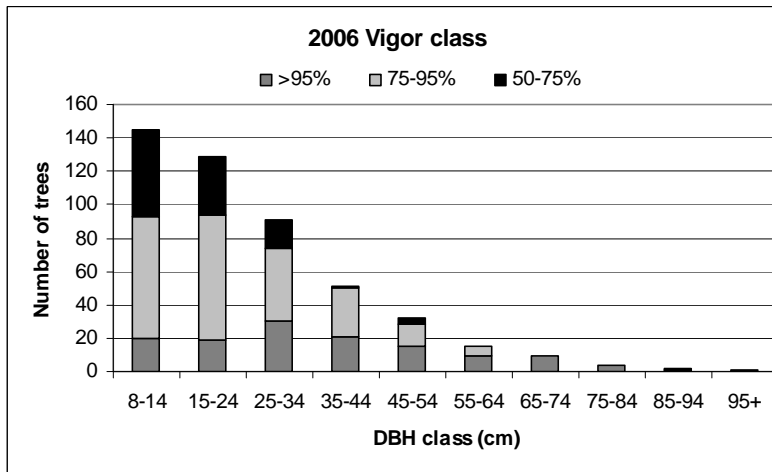
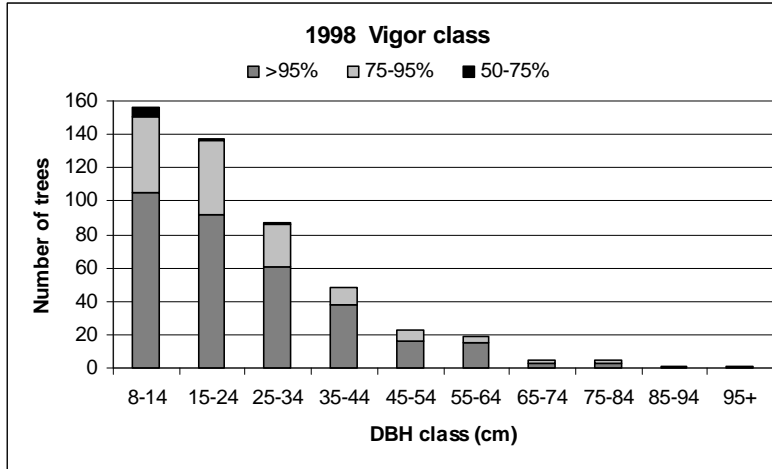


Figure 2. Number of live hemlock trees assigned to each vigor and dbh class in 1998, 2006, and 2007.

effects in statistical analyses. However, the four transects within each plot were considered random effects.

Percent cover of live trees and of live saplings and shrubs combined was estimated on the centerline of the four 10 m (32.8 ft) long belt transects per plot. At each decimeter along each transect (100 points per transect), presence/absence of tree and sapling/shrub cover was assigned to each vertical vegetation strata present in each plot (i.e., understory, shrub, low midstory, high midstory, subcanopy, canopy, supercanopy). Wood (1999a) includes detailed sampling methods and diagrams. The average maximum and minimum heights of each of seven vertical strata were estimated for each transect at the time of sampling. This method of estimating the height of vegetative strata has been used effectively by The Nature Conservancy in community-classification sampling and captured the structural diversity measures important to avian species. Cover of hemlock, other conifer, and hardwood trees in the seven strata were tallied separately, as was evergreen and deciduous sapling/shrub cover. We used a fixed-effects model ANOVA to compare tree and shrub cover for each strata between years and accounted for geographic location, soil moisture class, plot replicate, and transect as described above.

Avian Sampling and Analyses

The center of each vegetation sampling plot served as the center of the bird point count station. During 1999–2008, songbird richness and abundance were quantified using standardized sampling protocols on circular point count plots (Ralph et al. 1993) within a 50-m (164-ft) radius and at an unlimited distance. All birds seen or heard from one-half hour after sunrise to 1030 hours during appropriate weather conditions were recorded. Each count lasted 10 minutes and was conducted twice during the breeding season to detect both early and late arriving migrant breeders. All points were sampled once during the first or second week of June, then each was re-sampled the third or fourth week of June. We attempted to have at least one week between the two samples at each point. All point count personnel were highly skilled in bird identification by sight and sound and in point count protocols.

We summarized annual avian richness and abundance on each plot using count data from an unlimited radius to increase sample size of detections and to avoid variability among observers in distance estimation (Wood 2004). Species richness was the yearly total number of different species detected, while relative abundance was the maximum number of individuals of a given species detected over the two sampling periods in each year (Duguay et al. 2001).

We examined yearly trends in avian species richness and abundance for songbird species with a general linear ANOVA model in which our primary variable of interest, year, was treated as a continuous variable, and we accounted for variability in the data due to geographic location and soil moisture class. For these analyses, we excluded species that are not well sampled by point count methods including raptors, corvids, and water birds. The remaining species were categorized into habitat (forest interior, interior-edge, and early successional) and nesting (canopy, subcanopy, shrub, ground, and cavity) guilds to examine abundance and species richness for each guild with an ANOVA model as described above.

Results and Discussion

Hemlock Stand Age

At the beginning of the study in 1998, hemlock tree ages ranged from 38–328 years based on three hemlock trees cored (one from each of the three largest diameter classes present) in each of the 36 plots. Average age of trees in the hydric plots (mean=156.3 years, range=66–328) was greater than mesic (mean=74.3, range=44–131) and xeric (mean=69.2, range=38–136) plots ($F=59.69$, $P=0.0001$). The hydric plots sampled in this study tended to be less accessible (rockier and further from existing roads) than the other plots, which likely contributed to their older stand age.

Average (\pm SE) diameter of live hemlock trees was similar in 1998 and 2007 (1998: $n=482$, mean=25.1 \pm 0.7 cm [9.9 \pm 0.3 in]; 2007: $n=478$, mean=26.4 \pm 0.8 cm [10.4 \pm 0.3 in]) and the distribution across diameter classes did not change (Cochran-Mantel-Haenszel statistic=1.2, $P=0.27$). About a third of the live hemlock trees in both years were in the smallest (8–14 cm [3.2–5.5 in]) dbh class (Figure 2). Largest trees occurred in the hydric plots where maximum dbh in 2007 was 99.0 cm (38.9 in), while the maximum dbh in mesic and xeric plots was 67.2 cm (26.5 in) and 65.5 cm (25.8 in), respectively.

HWA Infestation and Vigor of Live Hemlock Trees

In November 1998, no plots had hemlock trees with evidence of HWA infestation. By the time HWA was first detected on eight of the study plots in 2004 (Table 2), we had obtained five years of pre-infestation data on the hemlock trees. All individual trees with HWA in these eight plots had indices of 3, indicating low severity of infestation. In fall 2006, HWA was observed on 22 plots (Table 2) with 154 hemlock trees on these plots infested. In fall 2007, HWA was detected on 15 plots with 113 trees infested. HWA sampling was completed by a different observer in 2006 than in 2007 and at slightly different times of the year (2006: 10/31–12/20/06; 2007: 12/14/07–1/19/08); thus the differences in number of plots with HWA detections could have been due to observer differences in ability to detect HWA or to differences in visibility of HWA during different times of the year. Regardless, HWA has become more prevalent on the plots since 2004 (Table 2). Hemlock trees with HWA ranged in size from 8–74 cm (3–29 in) dbh in both years.

Mean HWA infestation rank in 2007 was 3.9 in hydric plots, 3.6 in mesic plots, and 3.7 in xeric plots (Table 3) indicating that xeric and mesic plots were infested more heavily (Cochran-Mantel-Haenszel statistic=131.88, $P<0.0001$). Xeric and mesic plots also were infested more often in both 2006 and 2007 (Figure 3). More than 20% of hemlock trees on both mesic and xeric plots in 2007 had light HWA infestation compared to ~5% on hydric plots (Figure 3).

Of the 518 hemlock trees tallied and measured during November 1998, 36 were dead. In fall 2007, 46 of 529 hemlock trees tallied were dead. Stem density of dead hemlock trees did not change across years ($F=0.56$, $P=0.46$). This limited hemlock tree mortality was not likely related to HWA infestation because infestation rates were relatively low and HWA had not been present on plots for enough time to kill trees.

Table 2. Plots with hemlock woolly adelgid (HWA) detected in 2004, 2006, and 2007, with mean HWA infestation rank per plot (4=none, 1=heavy infestation).

Study Sites	Plot ID ^a	Mean HWA Infestation Rank on Plots with HWA Detected		
		2004	2006	2007
Gauley River NRA				
Meadow River				
Hedrick's Creek	MH1		3.7	
	MH2	3.5	3.5	
	MH3			
Mt. Lookout Rd.				
	MM1			
	MM2		3.9	3.9
	MM3		3.8	3.9
Underwood Rd.				
	MX1			3.5
	MX2		3.9	
	MX3		3.9	
Gauley River (Carnifex Ferry Battlefield State Park)				
	CH1			
	CH2			3.9
	CH3			
	CM1		3.9	
	CM2			
	CM3			
	CX1			
	CX2		3.9	
	CX3			
New River Gorge NR North				
Fern Creek				
	FH1			
	FH2		3.9	
	FH3		3.3	
Ames Heights				
	FX1	3.0	2.5	3.0
	FX2			3.9
Wolf Creek	FX3	3.8	2.9	
	WH1		3.9	
	WH2		3.0	
	WH3			3.7
	WX1		2.1	3.5
	WX2	3.4	1.3	3.0
	WX3	3.8	2.3	3.0
	New River Gorge NR South			
Kate's Branch				
	KM1		3.7	3.9
	KM2		3.9	
	KM3		3.0	3.3
Grandview				
	GM1	3.3	3.3	2.6
	GM2	3.4	3.5	3.0
	GM3	3.9		3.0

^aPlot ID second letter code represents: H=hydric; M=mesic; X=xeric.

Table 3. Mean and standard error (SE) for hemlock woolly adelgid (HWA) infestation rank, hemlock crown vigor, and hemlock live crown ratio of live hemlock trees in 1998 and 2007.

Variable and Moisture Class	1998		2007	
	mean	SE	mean	SE
HWA infestation rank	4.0	0.00	3.7	0.02
hydric	4.0	0.00	3.9	0.02
mesic	4.0	0.00	3.6	0.04
xeric	4.0	0.00	3.7	0.04
Crown vigor	1.3	0.02	1.9	0.02
hydric	1.4	0.04	1.8	0.04
mesic	1.2	0.04	2.0	0.03
xeric	1.4	0.04	1.9	0.05
Live crown ratio	60.5	1.11	63.1	0.93
hydric	52.5	1.70	62.5	1.43
mesic	67.2	1.68	62.3	1.56
xeric	61.9	2.17	64.5	1.80

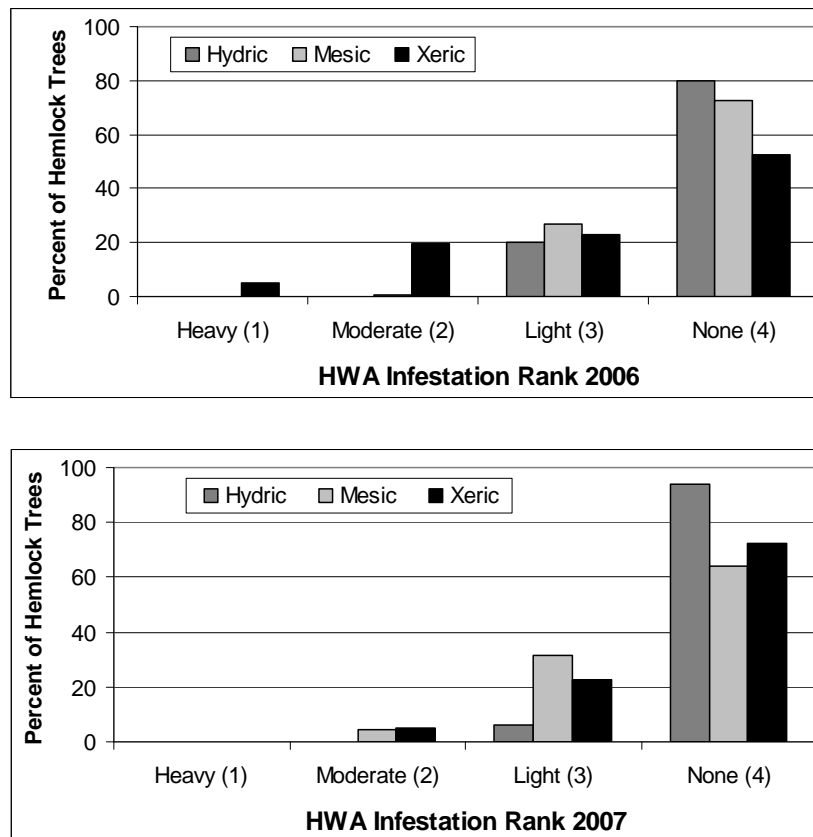


Figure 3. Percent of live hemlock trees in each HWA infestation rank by soil moisture class in fall 2006 (10/31–12/20/06) and fall 2007 (12/14/07–1/19/08).

In 1998, most live hemlocks appeared to be very healthy; 334 (69.3%) of the 482 live trees had >95% healthy crown, while only seven trees (1.5%) had vigor =3 (50–75% healthy crown). In 2006, crown health had appeared to decline as only 27% of 485 live hemlocks had >95% healthy crown. In 2007, trees with >95% healthy crown had declined to 16% of live hemlocks, while 7.3% of the 478 live trees had crown vigor =3 and two hemlocks were classed as vigor =4 (<50% healthy crown). Mean crown vigor declined for all three soil moisture classes between 1998 and 2007, particularly on the mesic plots (Table 3). The majority of low vigor trees were in the smallest dbh classes in both 2006 and 2007 (Figure 2). In 1998, the live crown ratio averaged $60.5 \pm 1.1\%$ and was similar to the 2007 ratio of $63.1 \pm 0.9\%$. Thus, although the amount of live crown had not changed appreciably, the health of the crowns appears to have declined over time. Hemlock tree crown size and vigor appear to have the strongest relationship with hemlock vulnerability to HWA (Rentch et al. 2009; Fajvan and Wood *in press*).

Stem Densities and Species Richness

Tree and sapling stem density of live hemlocks, tree stem density of live hardwoods, and shrub stem density of great laurel (*Rhododendron maximum*) did not change between 1999 and 2007 (Table 4). Although HWA infestation is beginning to affect hemlock crown vigor, it has not resulted in significant hemlock mortality or changes in live stem density. Stem density of deciduous shrubs and saplings declined slightly.

Species richness of hardwood tree stems was not different between 1999 and 2007 (Table 4), but did vary among the three soil moisture classes ($F=4.54$, $P=0.01$). Overall, the hydric moisture class had lowest mean richness of 4.5, while mesic and xeric moisture classes had mean richness of 5.8. Combined deciduous shrub and sapling species richness declined, although this may not be biologically significant as the mean per plot changed from 1.4 to 1.0 species. Over the two sampling periods, 28 tree species (Appendix A) and 23 shrub/sapling species (Appendix B) were recorded on the plots.

Table 4. Mean and standard error (SE) of stem density and species richness of different vegetative groups. Tree stems are ≥ 8 cm dbh; values are number per 400 m² plot. Shrub stems are ≥ 1.4 m in height and sapling stems are <8 cm dbh and ≥ 1.4 m in height; values are number per 20 m² transect. All sampling was completed summer 1999 and 2007, except hemlock tree stems were measured fall 1998 and 2007.

Variable and Vegetative Group	1999		2007		F	P
	mean	SE	mean	SE		
Stem density						
Hemlock trees	13.4	1.3	13.4	1.3	0.00	1.00
Hemlock saplings	1.1	0.2	0.9	0.2	1.54	0.22
Hardwood trees	13.2	1.0	11.7	1.1	1.47	0.23
Deciduous shrubs/hardwood saplings	4.9	0.5	4.0	0.4	4.27	0.04
Great laurel shrubs	2.8	0.4	2.7	0.4	0.11	0.74
Species richness						
Hardwood trees	5.6	0.4	5.0	0.4	2.08	0.15
Deciduous shrubs/hardwood saplings	1.4	0.1	1.0	0.1	11.38	0.0009

Vegetative Cover

Hemlock cover in some of the vegetative strata changed between 1999 and 2007 (Table 5). Cover in the canopy strata increased but decreased in the subcanopy, which might reflect growth of some trees into the canopy strata over the past eight years. The large increase in high midstory cover suggests that hemlock saplings also have grown substantially since 1999. In general, hemlock canopy and midstory cover appear to be increasing at this stage of HWA infestation and did not change enough to currently affect plant or wildlife communities.

Hardwood cover also changed in some of the vegetative strata between 1999 and 2007 (Table 5). Cover in the canopy and high midstory strata increased, which could reflect growth of some trees into these strata over the past eight years.

Cover of deciduous and evergreen shrub species that occurred in the shrub layer and understory did not change significantly between 1999 and 2007 (Table 5). Although hardwood tree cover in the shrub layer and understory strata decreased statistically, the percent change is low and not likely biologically significant.

Table 5. Vegetative cover (%) in seven vertical strata during summer 1999 and 2007.

Vegetative Group and Strata	1999		2007		F	P
	mean	SE	mean	SE		
Hemlock trees						
canopy	30.3	3.2	41.3	3.2	7.51	0.007
subcanopy	37.2	3.1	27.8	2.9	5.74	0.02
high midstory	2.8	0.9	31.5	2.6	113.90	<0.0001
low midstory	14.5	2.0	17.8	2.2	1.33	0.25
shrub	8.3	1.2	7.6	1.1	0.22	0.64
understory	5.0	1.0	2.7	0.6	4.65	0.03
Evergreen shrubs and saplings						
low midstory	0.0	0.0	8.2	1.2	62.25	<0.0001
shrub	15.2	1.7	13.4	1.7	1.01	0.32
understory	18.5	1.9	18.4	2.1	0.00	0.96
Hardwood trees						
supercanopy	1.2	0.8	2.9	1.3	1.28	0.26
canopy	55.2	3.4	71.5	2.9	19.88	<0.0001
subcanopy	20.5	2.3	17.1	2.3	1.17	0.28
high midstory	1.4	0.6	7.9	1.5	17.83	<0.0001
low midstory	5.3	1.2	2.8	0.8	3.26	0.07
shrub	2.3	0.6	0.8	0.3	5.34	0.02
understory	1.7	0.3	0.7	0.2	12.53	0.0005
Deciduous shrubs and hardwood saplings						
shrub	0.4	0.2	0.0	0.0	3.21	0.07
understory	0.3	0.1	0.1	0.1	3.49	0.06

Avian Richness and Abundance

During 1999–2008, seventy-six different avian species were detected on and adjacent to the sampling plots (Appendix A). Songbird species were the majority (65) and were used for statistical analyses.

Overall species richness of songbirds declined over time, as did richness and abundance of the forest interior and interior-edge habitat guilds (Figure 4) and the majority of nesting guilds (Table 6). In contrast, species richness and abundance of the early successional habitat guild had increasing trends as did species richness of the shrub nesting guild. The limited changes detected in vegetation structure on the plots suggest that changes in the bird community were not likely related to changes in vegetation structure but were due to other factors.

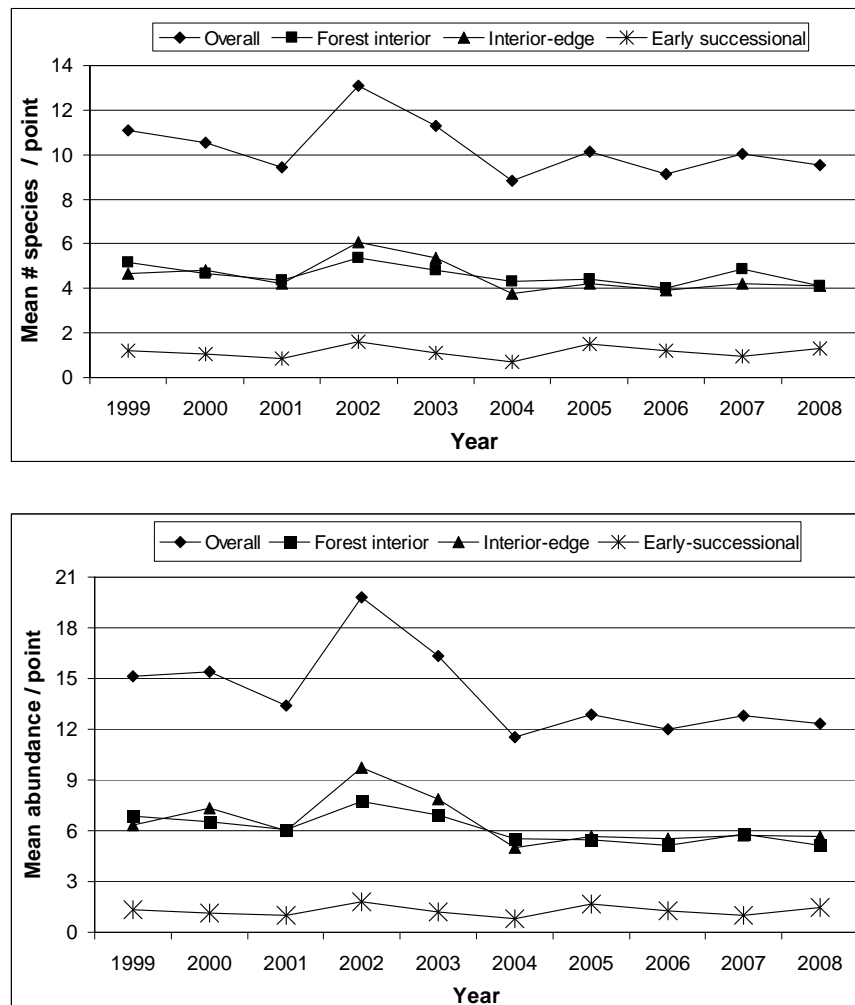


Figure 4. Annual trends in avian species richness and abundance (mean maximum abundance per point) overall and for habitat guilds.

Becker et al. (2007) found that only two bird species in their study, the acadian flycatcher (*Empidonax virescens*) and black-throated green warbler (*Dendroica virens*), were positively associated with living hemlocks. These two species are considered to be strong hemlock associates and are sensitive to hemlock removal (Tingley et al. 2002). In our study, both of these species had declining trends (Figure 5; Table 6). In contrast, Becker et al. (2007) found that wood thrush (*Hylocichla mustelina*) were negatively associated with the amount of living hemlocks and they suggested that this species was benefiting from the increased number of dead trees and canopy gaps that resulted from HWA infestation on their study areas. In our study, wood thrush abundance had increased slightly from the early years of our study (Table 6; Figure 5). Statewide in West Virginia, these three species have had varying trends based on Breeding Bird Survey data; acadian flycatchers and wood thrush have declining trends, while black-throated green warblers have been increasing (Sauer et al. 2007).

Summary and Conclusions

In 2004, eight of the 36 hemlock monitoring plots were infested with HWA. In 2006 and 2007, 27 of the plots had trees that showed signs of HWA infestation during at least one of those years. Hemlock tree mortality can occur within four to six years of infestation (McClure 1991); thus, we expect hemlock mortality to begin occurring within the plots in the near future. Continued monitoring is critical for documenting the response of the hemlock ecosystem to HWA and to improve our understanding of the impacts of the decline or elimination of this habitat type. We suggest, however, that vegetation sampling occur every one to two years to better evaluate annual variation in vegetation characteristics and response to adelgid infestation. Additionally, incorporating sampling of invasive species would provide important information on the timing of invasion by these species.

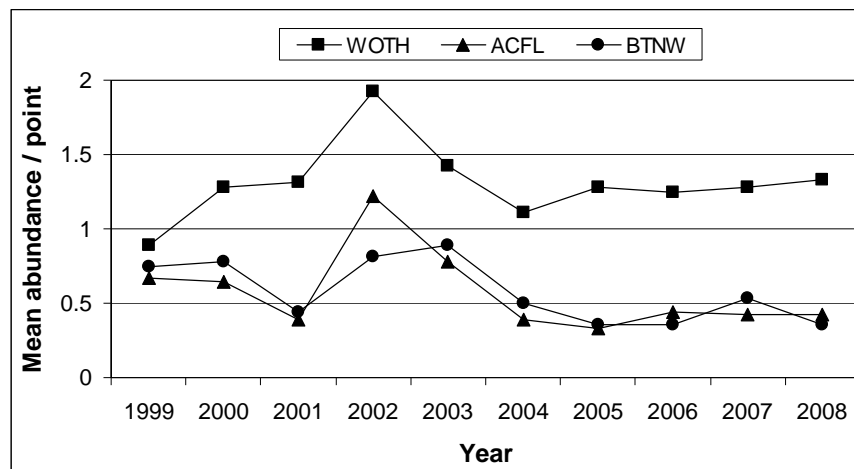


Figure 5. Annual trends in abundance (mean maximum per point) of acadian flycatchers (ACFL), black-throated green warblers (BTNW), and wood thrush (WOTH).

Table 6. Average annual songbird species richness (total number of species detected per point) and relative abundance (maximum number of individuals per point), and direction of annual trend of songbird detections during 1999–2008.

Guilds and Species	Mean	SE	Yearly trend			
			R ²	F	p	direction
Overall						
Species richness	10.31	0.17	0.55	10.14	<0.0001	-
Abundance	14.17	0.26	0.60	20.48	<0.0001	-
Habitat guilds						
Forest Interior						
Species richness	4.62	0.09	0.39	3.40	<0.001	-
Abundance	6.13	0.14	0.50	7.04	<0.0001	-
Interior-edge						
Species richness	4.53	0.10	0.44	8.26	<0.0001	-
Abundance	6.48	0.15	0.49	14.70	<0.0001	-
Early successional						
Species richness	1.15	0.06	0.49	3.33	<0.001	+
Abundance	1.26	0.07	0.48	3.39	<0.001	+
Nesting Guilds						
Subcanopy						
Species richness	2.86	0.06	0.48	2.40	0.012	-
Abundance	4.26	0.12	0.63	11.69	<0.0001	-
Canopy						
Species richness	2.24	0.06	0.48	5.75	<0.0001	-
Abundance	2.78	0.08	0.47	6.99	<0.0001	-
Shrub						
Species richness	1.46	0.05	0.47	2.62	0.006	+
Abundance	2.00	0.07	0.50	3.70	<0.001	-
Ground						
Species richness	1.72	0.05	0.32	2.23	0.020	-
Abundance	2.55	0.07	0.37	3.02	0.002	-
Cavity						
Species richness	1.98	0.07	0.45	6.96	<0.0001	-
Abundance	2.24	0.09	0.45	7.64	<0.0001	-
Species abundance						
acadian flycatcher	0.57	0.042	0.57	8.16	<0.0001	-
American goldfinch	0.10	0.017	0.31	6.55	<0.0001	-
American redstart	0.03	0.008	0.25	3.48	<0.001	-
American robin	0.16	0.022	0.34	0.73	0.677	
black-and-white warbler	0.29	0.025	0.38	2.13	0.027	+
black-capped chickadee	0.05	0.016	0.23	4.03	<0.0001	-
blue-gray gnatcatcher	0.00	0.003	0.17	1.00	0.440	
brown-headed cowbird	0.04	0.012	0.24	1.99	0.040	-
blue-headed vireo	0.66	0.037	0.34	2.24	0.020	+
blue jay	0.58	0.041	0.31	1.04	0.408	
brown creeper	0.00	0.003	0.17	1.00	0.440	
black-throated blue warbler	0.06	0.012	0.28	2.43	0.011	+
black-throated green warbler	0.58	0.036	0.58	6.30	<0.0001	-
blue-winged warbler	0.01	0.005	0.16	0.77	0.642	
Carolina chickadee	0.30	0.033	0.26	5.04	<0.0001	-
Carolina wren	0.31	0.029	0.33	2.96	0.002	+

Guilds and Species	Mean	SE	Yearly trend			direction
			R ²	F	p	
Canada warbler	0.01	0.004	0.25	2.20	0.022	-
cedar waxwing	0.01	0.005	0.16	1.51	0.144	
cerulean warbler	0.02	0.007	0.23	4.19	<0.0001	-
chipping sparrow	0.02	0.007	0.28	1.38	0.199	
chimney swift	0.01	0.005	0.16	0.77	0.642	
common yellowthroat	0.04	0.012	0.54	1.57	0.125	
chestnut-sided warbler	0.01	0.004	0.17	0.89	0.536	
dark-eyed junco	0.02	0.009	0.17	1.75	0.078	
downy woodpecker	0.08	0.015	0.21	2.28	0.017	-
eastern bluebird	0.00	0.003	0.17	1.00	0.440	
eastern meadowlark	0.00	0.003	0.17	1.00	0.440	
eastern phoebe	0.09	0.016	0.29	2.52	0.008	-
eastern towhee	0.18	0.023	0.36	2.04	0.035	-
eastern tufted titmouse	0.54	0.035	0.27	3.38	<0.001	-
eastern wood pewee	0.13	0.020	0.42	4.00	<0.0001	-
field sparrow	0.02	0.008	0.49	1.00	0.440	
great crested flycatcher	0.06	0.013	0.24	1.15	0.325	
golden-crowned kinglet	0.00	0.003	0.17	1.00	0.440	
gray catbird	0.00	0.003	0.17	1.00	0.440	
hairy woodpecker	0.13	0.019	0.24	3.68	<0.001	-
hooded warbler	1.27	0.050	0.50	2.78	0.004	-
indigo bunting	0.07	0.014	0.44	0.68	0.726	
Kentucky warbler	0.02	0.008	0.18	1.38	0.197	
Louisiana waterthrush	0.07	0.014	0.27	2.21	0.021	+
mourning dove	0.05	0.012	0.21	1.34	0.217	
northern cardinal	0.31	0.027	0.30	2.27	0.018	+
northern flicker	0.09	0.015	0.20	2.91	0.003	-
northern parula	0.34	0.028	0.52	2.87	0.003	-
Ovenbird	1.45	0.064	0.71	2.54	0.008	-
pine warbler	0.01	0.005	0.23	0.84	0.580	
pileated woodpecker	0.29	0.028	0.21	1.10	0.361	
rose-breasted grosbeak	0.01	0.006	0.20	0.70	0.710	
red-breasted nuthatch	0.00	0.003	0.17	1.00	0.440	
red-bellied woodpecker	0.09	0.016	0.40	2.61	0.006	-
red-eyed vireo	1.35	0.050	0.48	11.02	<0.0001	-
ruby-throated hummingbird	0.01	0.005	0.16	0.77	0.642	
red-winged blackbird	0.00	0.003	0.17	1.00	0.440	
scarlet tanager	1.04	0.037	0.31	2.37	0.013	-
song sparrow	0.06	0.015	0.70	0.96	0.475	
summer tanager	0.01	0.005	0.16	0.77	0.642	
Swainson's warbler	0.34	0.030	0.38	1.15	0.329	
veery	0.01	0.004	0.17	0.89	0.536	
white-breasted nuthatch	0.26	0.027	0.38	2.87	0.003	-
worm-eating warbler	0.16	0.022	0.48	4.89	<0.0001	-
winter wren	0.02	0.008	0.27	1.54	0.132	
wood thrush	1.31	0.059	0.51	3.29	<0.001	+
yellow-billed cuckoo	0.07	0.014	0.19	1.50	0.146	
yellow-throated vireo	0.04	0.011	0.28	2.68	0.005	-
yellow-throated warbler	0.04	0.011	0.20	1.51	0.142	

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Appendix A. Species of tree stems (≥ 8 cm [3.15 in] dbh) detected on 36 plots during summer 1999 and 2007 at Gauley River National Recreation Area and New River Gorge National River.

Tree species	1999		2007	
	Number of stems	Number of plots	Number of stems	Number of plots
<i>Acer pensylvanicum</i>	1	1	0	0
<i>Acer rubrum</i>	71	26	65	22
<i>Acer saccharum</i>	8	4	3	3
<i>Acer spicatum</i>	3	2	0	0
<i>Betula alleghaniensis</i>	4	3	4	2
<i>Betula lenta</i>	95	24	77	21
<i>Carya glabra</i>	10	7	9	6
<i>Carya ovata</i>	1	1	2	2
<i>Carya tomentosa</i>	7	3	4	3
<i>Cornus florida</i>	1	1	0	0
<i>Fagus grandifolia</i>	14	11	16	14
<i>Ilex opaca</i>	6	4	7	4
<i>Liriodendron tulipifera</i>	70	18	67	19
<i>Magnolia acuminata</i>	5	5	5	5
<i>Magnolia fraseri</i>	11	6	11	8
<i>Nyssa sylvatica</i>	15	8	11	5
<i>Oxydendrum arboreum</i>	31	15	22	12
<i>Pinus strobus</i>	4	2	4	2
<i>Pinus virginiana</i>	3	1	0	0
<i>Prunus serotina</i>	6	4	4	2
<i>Quercus alba</i>	32	12	29	12
<i>Quercus coccinea</i>	3	2	4	2
<i>Quercus prinus</i>	19	9	18	9
<i>Quercus rubra</i>	27	14	25	13
<i>Quercus velutina</i>	15	11	10	4
<i>Rhododendron maximum</i>	7	4	9	3
<i>Sassafras albidum</i>	2	1	1	1
<i>Tilia americana</i>	3	3	3	3
Total stems	474		410	

Appendix B. Species of shrub (≥ 1.4 m [4.6 ft] in height) and sapling (< 8 cm [3.15 in] dbh and ≥ 1.4 m [4.6 ft] in height) stems detected on 144 belt transects on the 36 plots during summer 1999 and 2007 at Gauley River National Recreation Area and New River Gorge National River.

Tree species	1999		2007	
	Number of stems	Number of plots	Number of stems	Number of plots
<i>Acer pensylvanicum</i>	1	1	0	0
<i>Acer rubrum</i>	15	9	6	6
<i>Betula alleghaniensis</i>	0	0	3	1
<i>Betula lenta</i>	4	4	1	1
<i>Carya glabra</i>	1	1	0	0
<i>Clethra acuminata</i>	7	7	0	0
<i>Fagus grandifolia</i>	17	16	13	12
<i>Hamamelis virginiana</i>	23	11	12	6
<i>Ilex montana</i>	7	4	0	0
<i>Ilex opaca</i>	10	8	9	8
<i>Kalmia latifolia</i>	5	2	3	3
<i>Liriodendron tulipifera</i>	14	8	1	1
<i>Magnolia fraseri</i>	13	13	5	5
<i>Magnolia tripetala</i>	1	1	0	0
<i>Nyssa sylvatica</i>	7	6	2	2
<i>Oxydendrum arboreum</i>	4	4	1	1
<i>Prunus pensylvanica</i>	2	1	0	0
<i>Prunus serotina</i>	2	2	0	0
<i>Rhododendron maximum</i>	407	118	390	120
<i>Rhus glabra</i>	1	1	0	0
<i>Sassafras albidum</i>	2	2	0	0
<i>Tsuga canadensis</i>	163	75	124	58
<i>Vitis aestivalis</i>	1	1	0	0
Unknown	0	0	1	1
Total stems	707		571	

Appendix C. Avian species detected with unlimited radius on 36 point counts from 1999–2008 at Gauley River National Recreation Area and New River Gorge National River.

Common name	Scientific name	Average annual number of detections				Average annual number of points where species was detected				Guilds ^a	
		mean	SE	min.	max.	mean	SE	min.	max.	Habitat	Nesting
acadian flycatcher	<i>Empidonax vireescens</i>	20.5	3.10	12	44	14.7	1.51	10	25	FI	SC
American crow	<i>Corvus brachyrhynchos</i>	29.3	2.56	16	41	19.2	1.13	14	26		
American goldfinch	<i>Carduelis tristis</i>	3.5	1.40	0	14	3.3	1.28	0	13	ES	SH
American redstart	<i>Setophaga ruticilla</i>	0.9	0.53	0	5	0.9	0.53	0	5	IE	SC
American robin	<i>Turdus migratorius</i>	5.6	0.60	3	9	4.9	0.46	3	7	EI	SC
black-and-white warbler	<i>Mniotilta varia</i>	10.4	1.12	4	16	10.2	1.06	4	16	FI	GG
black-capped chickadee	<i>Poecile atricapillus</i>	1.8	1.15	0	12	1.3	0.67	0	7	IE	HH
barred owl	<i>Strix varia</i>	0.9	0.31	0	3	0.8	0.25	0	2		
belted kingfisher	<i>Ceryle alcyon</i>	0.1	0.10	0	1	0.1	0.10	0	1		
blue-gray gnatcatcher	<i>Poliptila caerulea</i>	0.1	0.10	0	1	0.1	0.10	0	1	IE	SC
brown-headed cowbird	<i>Molothrus ater</i>	1.6	0.56	0	5	1.5	0.54	0	5	IE	PA
blue-headed vireo	<i>Vireo solitarius</i>	23.8	1.76	14	32	19.6	1.13	14	26	FI	SC
blue jay	<i>Cyanocitta cristata</i>	20.7	1.37	16	31	15.4	0.99	12	22	IE	CA
brown creeper	<i>Certhia americana</i>	0.1	0.10	0	1	0.1	0.10	0	1	FI	SC
black-throated blue warbler	<i>Dendroica caerulescens</i>	2.0	0.63	0	6	2.0	0.63	0	6	FI	SH
black-throated green warbler	<i>Dendroica virens</i>	20.8	2.36	13	32	16.9	1.20	12	23	FI	CA
blue-winged warbler	<i>Verminora pinus</i>	0.3	0.15	0	1	0.3	0.15	0	1	ES	GG
Carolina chickadee	<i>Poecile carolinensis</i>	10.8	2.56	3	25	8.4	1.82	3	19	IE	HH
Canada goose	<i>Branta canadensis</i>	0.4	0.27	0	2	0.2	0.13	0	1		
Carolina wren	<i>Thryothorus ludovicianus</i>	11.1	1.60	2	18	9.8	1.40	2	16	ES	HH
Canada warbler	<i>Wilsonia canadensis</i>	0.2	0.20	0	2	0.2	0.20	0	2	IE	GG
cedar waxwing	<i>Bombycilla cedrorum</i>	0.3	0.21	0	2	0.3	0.21	0	2	IE	SC
cerulean warbler	<i>Dendroica cerulea</i>	0.7	0.52	0	5	0.7	0.52	0	5	FI	CA
chipping sparrow	<i>Spizella passerina</i>	0.6	0.27	0	2	0.6	0.27	0	2	ES	SH
chimney swift	<i>Chaetura pelagica</i>	0.3	0.15	0	1	0.3	0.15	0	1		
common raven	<i>Corvus corax</i>	1.5	0.52	0	5	1.4	0.50	0	5		

Common name	Scientific name	Average annual number of detections				Average annual number of points where species was detected				Guilds ^a	
		mean	SE	min.	max.	mean	SE	min.	max.	Habitat	Nesting
common yellowthroat	<i>Geothlypis trichas</i>	1.5	0.40	0	4	1.3	0.33	0	3	ES	SH
chestnut-sided warbler	<i>Dendroica pensylvanica</i>	0.2	0.13	0	1	0.2	0.13	0	1	ES	SH
dark-eyed junco	<i>Junco hyemalis</i>	0.8	0.42	0	4	0.7	0.33	0	3	IE	GG
downy woodpecker	<i>Picoides pubescens</i>	3.0	0.77	0	7	3.0	0.77	0	7	IE	HH
eastern bluebird	<i>Sialia sialis</i>	0.1	0.10	0	1	0.1	0.10	0	1	ES	HH
eastern meadowlark	<i>Sturnella magna</i>	0.1	0.10	0	1	0.1	0.10	0	1	GR	GG
eastern phoebe	<i>Sayornis phoebe</i>	3.4	0.85	0	8	3.3	0.83	0	8	ES	SC
eastern screech owl	<i>Otus asio</i>	0.1	0.10	0	1	0.1	0.10	0	1		
eastern towhee	<i>Pipilo erythrophthalmus</i>	6.5	1.04	3	14	5.8	0.81	3	12	ES	GG
eastern tufted titmouse	<i>Baeolophus bicolor</i>	19.6	2.20	9	30	16.9	1.66	9	26	IE	HH
eastern wood pewee	<i>Contopus virens</i>	4.7	1.22	1	11	4.1	0.91	1	9	FI	CA
field sparrow	<i>Spizella pusilla</i>	0.6	0.22	0	2	0.5	0.17	0	1	ES	SH
great crested flycatcher	<i>Myiarchus crinitus</i>	2.2	0.49	0	5	2.1	0.43	0	4	IE	HH
golden-crowned kinglet	<i>Regulus satrapa</i>	0.1	0.10	0	1	0.1	0.10	0	1	FI	CA
gray catbird	<i>Dumetella carolinensis</i>	0.1	0.10	0	1	0.1	0.10	0	1	ES	SH
hairy woodpecker	<i>Picoides villosus</i>	4.7	1.23	1	13	4.5	1.18	1	12	FI	HH
hooded warbler	<i>Wilsonia citrina</i>	45.8	2.33	34	56	28.2	0.92	24	33	IE	SH
indigo bunting	<i>Passerina cyanea</i>	2.5	0.34	1	4	2.4	0.34	1	4	ES	SH
Kentucky warbler	<i>Oporornis formosus</i>	0.8	0.33	0	3	0.8	0.33	0	3	FI	GG
Louisiana waterthrush	<i>Seiurus motacilla</i>	2.4	0.72	0	6	2.2	0.63	0	5	FI	GG
mallard	<i>Anas platyrhynchos</i>	0.1	0.10	0	1	0.1	0.10	0	1		
mourning dove	<i>Zenaida macroura</i>	1.8	0.47	0	5	1.8	0.47	0	5	ES	SH
northern cardinal	<i>Cardinalis cardinalis</i>	11.1	1.35	6	18	10.2	1.24	5	16	ES	SH
northern flicker	<i>Colaptes auratus</i>	3.1	0.92	0	9	3.0	0.86	0	8	IE	HH
northern parula	<i>Parula americana</i>	12.4	1.29	7	18	11.5	1.16	7	17	IE	CA
ovenbird	<i>Seiurus aurocapillus</i>	52.1	2.18	43	62	25.8	0.79	21	30	FI	GG
pine warbler	<i>Dendroica pinus</i>	0.3	0.15	0	1	0.3	0.15	0	1	IE	CA
pileated woodpecker	<i>Dryocopus pileatus</i>	10.6	1.02	7	16	9.6	0.72	7	13	FI	HH
rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	0.4	0.16	0	1	0.4	0.16	0	1	IE	SC

Common name	Scientific name	Average annual number of detections				Average annual number of points where species was detected				Guilds ^a	
		mean	SE	min.	max.	mean	SE	min.	max.	Habitat	Nesting
red-breasted nuthatch	<i>Sitta canadensis</i>	0.1	0.10	0	1	0.1	0.10	0	1	FI	HH
red-bellied woodpecker	<i>Melanerpes carolinus</i>	3.4	0.79	1	9	3.3	0.72	1	8	IE	HH
red-eyed vireo	<i>Vireo olivaceus</i>	48.6	4.68	34	81	30.1	1.11	26	36	IE	SC
red-shouldered hawk	<i>Buteo lineatus</i>	1.7	0.40	0	4	1.6	0.34	0	3		
red-tailed hawk	<i>Buteo jamaicensis</i>	0.1	0.10	0	1	0.1	0.10	0	1		
ruby-throated hummingbird	<i>Archilochus colubris</i>	0.3	0.15	0	1	0.3	0.15	0	1	IE	SC
red-winged blackbird	<i>Agelaius phoeniceus</i>	0.1	0.10	0	1	0.1	0.10	0	1	GR	SH
scarlet tanager	<i>Piranga olivacea</i>	37.4	1.89	29	47	28.8	1.13	23	35	FI	CA
song sparrow	<i>Melospiza melodia</i>	2.2	0.33	0	3	1.7	0.30	0	3	ES	SH
sharp-shinned hawk	<i>Accipiter striatus</i>	0.1	0.10	0	1	0.1	0.10	0	1		
summer tanager	<i>Piranga rubra</i>	0.3	0.15	0	1	0.3	0.15	0	1	IE	CA
Swainson's warbler	<i>Limnithlypis swainsonii</i>	12.1	0.99	8	18	10.5	0.86	6	14	FI	GG
turkey vulture	<i>Cathartes aura</i>	0.2	0.20	0	2	0.1	0.10	0	1		
veery	<i>Catharus fuscescens</i>	0.2	0.13	0	1	0.2	0.13	0	1	IE	GG
white-breasted nuthatch	<i>Sitta carolinensis</i>	9.3	1.41	3	16	8.2	1.06	3	12	FI	HH
worm-eating warbler	<i>Helmitheros vermivorus</i>	5.9	1.39	0	15	5.2	1.07	0	11	FI	GG
winter wren	<i>Troglodytes troglodytes</i>	0.8	0.33	0	3	0.8	0.33	0	3	FI	HH
wood thrush	<i>Hylocichla mustelina</i>	47.0	2.95	32	69	26.1	1.23	20	31	IE	SC
yellow-billed cuckoo	<i>Coccyzus americanus</i>	2.4	0.60	1	7	2.3	0.52	1	6	IE	SC
yellow-throated vireo	<i>Vireo flavifrons</i>	1.4	0.60	0	6	1.3	0.52	0	5	IE	CA
yellow-throated warbler	<i>Dendroica dominica</i>	1.4	0.48	0	4	1.3	0.42	0	4	FI	CA

^aSpecies with no listed guild assignments were excluded from statistical analyses because they were not well-sampled with point count methods. Statistical analyses were restricted to songbird species. Guild codes are:

Habitat: FI=forest interior; IE=interior-edge; ES=early successional

Nesting: CA=canopy; SC=subcanopy; SH=shrub; GG=ground; HH=cavity.

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