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SPECIAL FEATURE: SCIENCE FOR OUR NATIONAL PARKS' SECOND CENTURY

National parks in the eastern United States harbor important older forest structure compared with matrix forests

Kathryn M. Miller,[1,2,†] Fred W. Dieffenbach,[3] J. Patrick Campbell,[4] Wendy B. Cass,[5]
James A. Comiskey,[6] Elizabeth R. Matthews,[4] Brian J. McGill,[2] Brian R. Mitchell,[7]
Stephanie J. Perles,[8] Suzanne Sanders,[9] John Paul Schmit,[4] Stephen Smith,[10] and Aaron S. Weed[11]

[1]*National Park Service, Northeast Temperate Network, Bar Harbor, Maine 04609 USA*
[2]*School of Biology and Ecology, University of Maine, Orono, Maine 04469 USA*
[3]*National Park Service, Northeast Temperate Network, Woodstock, Vermont 05091 USA*
[4]*National Park Service, National Capital Region Network, Washington, D.C. 20007 USA*
[5]*National Park Service, Shenandoah National Park, Luray, Virginia 22835 USA*
[6]*National Park Service, Northeast Region Inventory and Monitoring Program, Fredericksburg, Virginia 22405 USA*
[7]*National Park Service, Southeast Regional Office, Atlanta, Georgia 30303 USA*
[8]*National Park Service, Eastern Rivers and Mountains Network, University Park, Pennsylvania 16802 USA*
[9]*National Park Service, Great Lakes Network, Ashland, Wisconsin 54806 USA*
[10]*National Park Service, Cape Cod National Seashore, Wellfleet, Massachusetts 02667 USA*
[11]*National Park Service, Mid-Atlantic Network, Fredericksburg, Virginia 22405 USA*

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Abstract. We analyzed land-cover and forest vegetation data from nearly 25,000 permanent plots distributed across 50 national parks in the eastern United States, along with the matrix around each park, to examine structural characteristics of park forests in relation to their surrounding landscape. Over 2000 of these plots are part of the National Park Service (NPS) Inventory and Monitoring Program (I&M), and the remaining 22,500+ plots are part of the US Forest Service (USFS) Forest Inventory and Analysis (FIA) Program. This is the first study to compare forest structure in protected lands with the surrounding forest matrix over such a large area of the United States and is only possible because of the 10+ years of data that are now publicly available from USFS-FIA and NPS I&M. Results of this study indicate that park forests, where logging is largely prohibited, preserve areas of regionally significant older forest habitat. Park forests consistently had greater proportions of late-successional forest, greater live tree basal area, greater densities of live and dead large trees, and considerably larger volume of coarse woody debris. Park forests also had lower tree growth and mortality rates than matrix forests, suggesting different forest dynamics between park and matrix forests. The divergent patterns we observed between matrix and park forests were similar to those reported in studies that compared managed and old-growth forests, although the differences in our study were less pronounced. With the majority of park forests in second growth, eastern parks may be a more realistic baseline to compare with the more intensively managed matrix forests. We recommend that park managers allow natural disturbance and the development of older structure to continue in park forests. In addition, long-term maintenance of regional biodiversity will likely require increases in older forest structure in the matrix. As the NPS moves into its next century of land preservation, we encourage managers to consider parks important components of a larger regional effort to preserve biodiversity and ecosystem processes in eastern US forests. The data collected by NPS I&M programs will continue to provide important information and guidance toward these regional conservation efforts.

Key words: Forest Inventory and Analysis; forest structure; long-term monitoring; National Park Service Inventory and Monitoring; Special Feature: Science for Our National Parks' Second Century; vital signs.

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† **E-mail:** kathryn_miller@nps.gov

INTRODUCTION

Forests in the eastern United States perform essential ecosystem services, provide food and habitat for countless organisms, and generate significant economic benefits to the region (Krieger 2001). Sustainable management of eastern forests is imperative to ensure long-term ecosystem health, maintain biodiversity, and provide a continual supply of forest products (Hunter 1999, Lindenmayer et al. 2000). Sustainable forestry approaches are typically designed to mimic natural disturbances, such as using single-tree or group selection to simulate gap dynamics in hardwood forests (Attiwill 1994, Pond et al. 2014). While these practices are an improvement ecologically over even-aged management, selective forestry still causes adverse effects on biodiversity, as it is somewhat limited in its ability to reproduce forest responses to natural disturbances, such as tip-up mounds and coarse woody debris (CWD; Simard and Fryxell 2003). For example, single-tree selection in northern hardwood forests favors sugar maple (*Acer saccharum*) regeneration over tree species which require exposed mineral soil or CWD to germinate, resulting in an overall decrease in tree diversity over time (Neuendorff et al. 2007). Selective forestry practices also reduce abundance of dead wood and large-diameter trees compared with unmanaged forests (Goodburn and Lorimer 1998, Hale et al. 1999). Dead wood, including dead standing trees (snags) and CWD, is a vital structural component of forests for many organisms, including small mammals (Fauteux et al. 2012), birds (Conner et al. 1994), invertebrates (Grove 2002, Janssen et al. 2011), fungi (Kebli et al. 2011, Dove and Keeton 2015), amphibians (deMaynadier and Hunter 1995), lichens (Spribille et al. 2008), and tree seedlings (Bolton and D'Amato 2011). Additionally, large-diameter live and dead trees are preferentially occupied over small-diameter trees by a range of vertebrate species (Renken and Wiggers 1989, Lacki et al. 2007). In northern European forests, widespread reduction in these structural components from decades to centuries of commercial forestry has caused dramatic declines in many forest species to the extent that nearly two-thirds of red-listed (equivalent to Rare, Threatened, and Endangered status in the United States) forest-dwelling species in Finland and Sweden are species that are dependent on dead wood (Berg et al. 1994, Tikkanen et al. 2006). The trends in northern Europe underscore the need to ensure that forestry practices in the eastern United States maintain these important structural features to prevent similar species declines.

As suggested by Lindenmayer et al. (2000), continual improvement in sustainable forestry practices requires long-term monitoring, not only of areas that are managed for timber, but also of forested areas that are protected from harvesting. Comparisons between the two groups can highlight both the direct and indirect impacts of harvest and help identify aspects of forestry practices that are successful or need improvement. Large-scale, long-term monitoring programs focused on areas that are protected from logging have been lacking for eastern forests. The US Forest Service (USFS) Forest Inventory and Analysis (FIA) program, which employs permanent plots located across the conterminous United States to monitor status and trends in forest area, timber volume, and forest health, has made important contributions to our understanding of eastern forests (Woodall et al. 2011). However, the majority of forests monitored by USFS-FIA are not reserved from timber production (Oswalt et al. 2014). The establishment of the National Park Service (NPS) Inventory and Monitoring (I&M) program provides a new opportunity to examine forests where logging is largely prohibited and can serve as important benchmarks (i.e., references) to compare with the more intensively managed forests in the eastern United States.

The NPS I&M program conducts long-term monitoring of ecological indicators in over 270 national parks with significant natural resources, and a primary responsibility of NPS I&M is to use long-term monitoring data to inform resource management decisions in parks. From the outset,

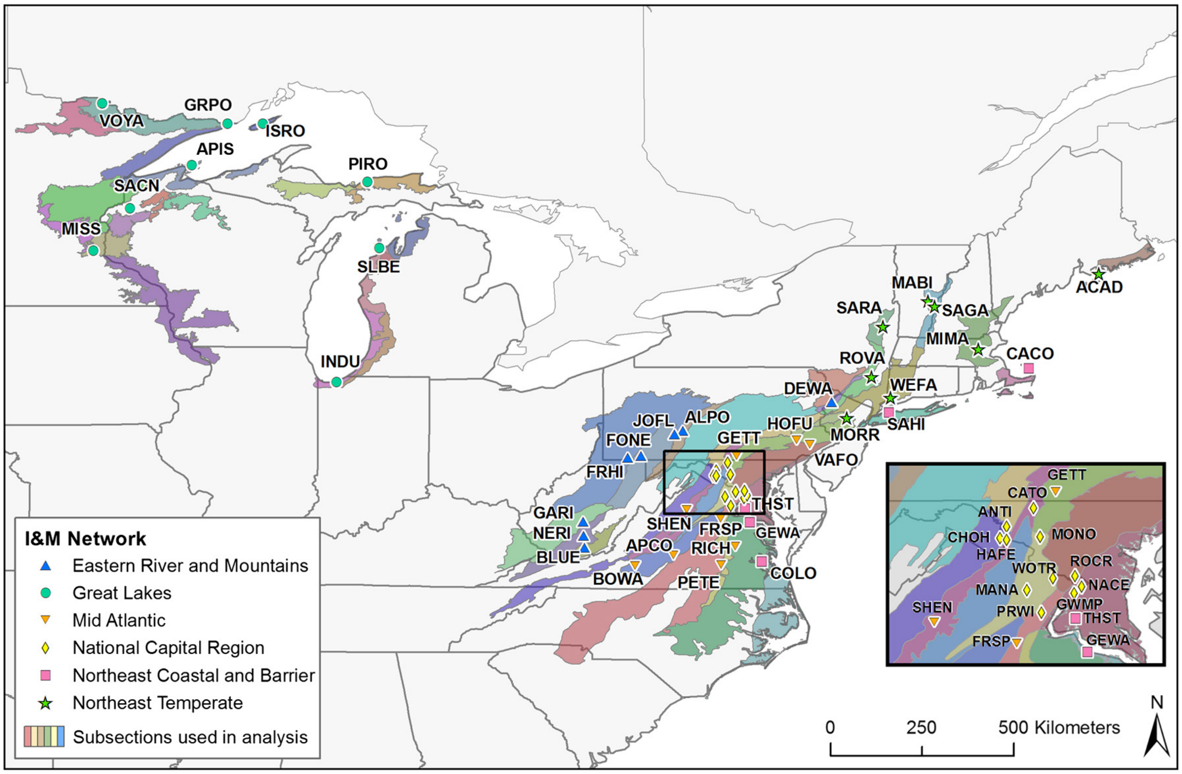

Fig. 1. Map of national parks and Ecological Subsections that were included in this study. See Table 1 for full park names.

parks in the NPS I&M program were grouped into 32 networks based on their proximity and similar natural resources, and each network is responsible for monitoring a specific set of indicators in their respective parks (Fancy et al. 2009). In the eastern United States, six NPS I&M networks covering 50 parks have been monitoring forests in permanent plots for a decade or more using methods adapted from USFS-FIA protocols and that are relatively standard across networks (Fig. 1; Comiskey et al. 2009*a*). The forest data collected by the NPS I&M program are publicly available and represent the most extensive data to date on eastern forests that are protected from logging.

In addition to serving as benchmarks for comparisons with more intensively managed forests, park forests may be important sites of biodiversity. Even small urban parks that are protected have been shown to support greater diversity of breeding birds than unprotected areas (Goodwin and Shriver 2014), and small preserves have successfully protected rare plant species with narrow distributions (Parker 2012). However, national park units and other reserves only represent a small portion of the landscape, and park managers likely need to consider a larger landscape that extends beyond the boundary of parks to successfully maintain biodiversity (Keeton 2007). This is especially true, given that climate change will likely shift suitable habitat of currently common park species outside of park boundaries (Rustad et al. 2012). Therefore, understanding the characteristics of the landscape surrounding parks, such as land-use and ownership patterns, along with the attributes of surrounding forestlands, may reveal how park forests are unique and potentially valuable components of the landscape, provide insights into how to better manage park and surrounding forests, and indicate how the regional landscape may influence park forests.

In this study, our primary questions are whether the protection status (i.e., protected from logging) of parks is unique in the region and whether this has resulted in structural differences compared with surrounding unprotected forests, which we refer to in the conservation biology context as matrix forests (Lindenmayer and Franklin 2002). Forests, both in eastern parks and in surrounding lands, are largely second growth and share similar land-use histories (e.g., logging, clearing for agriculture) prior to the establishment of the parks; therefore, differences between park and matrix forests are likely due to different management practices. We first describe patterns of land cover and ownership in the matrix surrounding each of 50 parks in the eastern United States, represented by the Ecological Subsection (US Forest Service 2015*a*) that surrounds or is intersected by a park. We then compared metrics of forest structure from data collected by I&M networks in parks with data collected by the USFS-FIA program in plots located in the Ecological Subsection surrounding each park. We focus on metrics of forest structure because they are straightforward to calculate and scale up across the different monitoring protocols; further, we chose structural metrics that have been used by previous studies to document forest structure relative to different management practices (e.g., Goodburn and Lorimer 1998, Hale et al. 1999) or habitat requirements for wildlife (e.g., Renken and Wiggers 1989, Lacki and Cox 2009). We also included several metrics that are commonly reported in USFS-FIA state reports (e.g., live tree basal area, mortality rate) to demonstrate the compatibility of NPS I&M data for comparisons with USFS-FIA (e.g., McCaskill 2015). This is the first study to compare forest structure in protected lands with the surrounding forest matrix over such a large area of the United States and is only possible because of the 10+ years of data that are now publicly available from USFS-FIA and NPS I&M.

METHODS

Site selection

This study included 50 national parks across six NPS I&M networks (Fig. 1). Parks in the study were diverse in size and in mission, such as National Parks (NP), National Battlefield Parks (NBP), National Historical Parks (NHP), National Historic Sites (NHS), and National Lakeshores (NL; Table 1). Forests in this study range from the northern hardwood and boreal forests of the Great Lakes region and northern New England, to the urban landscapes along the east coast. Parks range in size from 80,562 ha in Shenandoah NP (SHEN) to 28 ha in Weir Farm NHS (WEFA). Parks range in the extent of forest within their boundaries, although all were determined to have sufficient forest resources by NPS I&M networks to warrant long-term monitoring (Table 1; Comiskey et al. 2009*a*). Battlefield parks, such as Gettysburg National Military Park (GETT; NMP), Manassas NBP (MANA), and Saratoga NHP (SARA), are often comprised of a patchwork of open field and forest. In contrast, many of the larger parks, such as SHEN, Isle Royale NP (ISRO), Voyageurs NP (VOYA), and New River Gorge National River (NERI; NR), are predominantly forested. Some parks have been protected for more than a century (e.g., Rock Creek Park [ROCR]) and others for less than two decades (e.g., Marsh-Billings-Rockefeller NHP [MABI]). All parks in this study have active forest monitoring programs employing compatible methods, both among NPS I&M networks and with the USFS-FIA Program (Comiskey et al. 2009*a*). For example, while plot designs may vary, all NPS I&M networks measure tree diameter at breast height (DBH) for all trees that are at least 10 cm DBH on each plot. NPS I&M networks used generalized random-tessellation stratification (GRTS) to generate a spatially balanced and randomized sample of permanent forest plot locations for the parks in this study (Stevens and Olsen 2004). The GRTS sample design allows NPS I&M networks to develop a representative sample of randomly located forest plots to characterize status and trends in forest vegetation within each park (Comiskey et al. 2009*a*). Similar to USFS-FIA, NPS I&M uses a rotating panel design, whereby plots are sampled on a 4- or 5-year cycle (depending on the network) with one panel of plots sampled each year. For this analysis, we used the most recent complete set of forest plot surveys for each park, which typically was 2011–2014, but ranged from 2008 to 2015. For more details on NPS I&M sample design and survey methods, refer to network and/or park-specific protocols (Comiskey et al. 2009*b*, Cass et al. 2011, Smith et al. 2011, Perles et al. 2014, Sanders and Grochowski 2014, Schmit et al. 2014, Tierney et al. 2015).

Table 1. Information on NPS I&M networks and parks in this study.

Network	Code	Park area (ha)	
		Total	Forest
Eastern Rivers and Mountains Network	ERMN		
Allegheny Portage Railroad National Historic Site (NHS)	ALPO	503	430
Bluestone National Scenic River (NSR)	BLUE	1236	1144
Delaware Water Gap National Recreation Area (NRA)	DEWA	22,839	19,313
Fort Necessity National Battlefield (NB)	FONE	373	276
Friendship Hill National Historic Site (NHS)	FRHI	280	224
Gauley River NRA	GARI	1930	1779
Johnstown Flood National Memorial (NMe)	JOFL	72	23
New River Gorge National River (NR)	NERI	21,528	19,615
Great Lakes	GLKN		
Apostle Islands National Lakeshore (NL)	APIS	17,016	16,912
Grand Portage National Monument (NMo)	GRPO	287	259
Indiana Dunes NL	INDU	6073	5542
Isle Royale National Park (NP)	ISRO	54,130	49,468
Mississippi National River and Recreation Area (NRRA)	MISS	21,853	4802
Pictured Rocks NL	PIRO	29,638	27,538
Saint Croix National Scenic River (NSR)	SACN	33,095	19,097
Sleeping Bear Dunes NL	SLBE	28,821	27,242
Voyageurs NP	VOYA	52,227	50,171
Mid-Atlantic Network	MIDN		
Appomattox Court House National Historical Park (NHP)	APCO	687	442
Booker T. Washington NMo	BOWA	100	62
Fredericksburg & Spotsylvania National Military Park (NMP)	FRSP	3056	2180
Gettysburg NMP	GETT	1743	548
Hopewell Furnace NHS	HOFU	343	270
Petersburg NB	PETE	1092	923
Richmond National Battlefield Park (NBP)	RICH	819	585
Shenandoah NP	SHEN	80,562	79,781
Valley Forge NHP	VAFO	1395	538
Northeast Coastal and Barrier Network	NCBN		
Cape Cod National Seashore (NS)	CACO	8755	6188
Colonial NHP	COLO	2219	1471
George Washington Birthplace NMo	GEWA	216	87
Sagamore Hill NHS	SAHI	29	17
Thomas Stone NHS	THST	179	123
National Capital Region Network	NCRN		
Antietam NB	ANTI	759	129
Catoctin Mountain Park	CATO	2282	2237
Chesapeake and Ohio Canal NHP	CHOH	5980	4261
George Washington Memorial Parkway	GWMP	1661	969
Harpers Ferry NHP	HAFE	1480	1091
Manassas NBP	MANA	1727	784
Monocacy NB	MONO	530	132
National Capital Parks East	NACE	3088	1942
Prince William Forest Park	PRWI	5089	4899
Rock Creek Park	ROCR	1061	812
Wolf Trap Park for the Performing Arts	WOTR	43	26
Northeast Temperate Network	NETN		
Acadia National Park	ACAD	14,577	8178
Marsh-Billings-Rockefeller NHP	MABI	223	196
Minute Man NHP	MIMA	391	234
Morristown NHP	MORR	676	626
Roosevelt-Vanderbilt NHS	ROVA	446	338
Saint-Gaudens NHS	SAGA	80	48
Saratoga NHP	SARA	1156	687
Weir Farm NHS	WEFA	28	18

Matrix characterization

To represent the matrix for each park, we selected data from all USFS-FIA plots that were located within the Ecological Subsection(s) that surrounded and/or intersected each individual park (Table 2). Ecological Subsections are contiguous areas that have the same potential natural vegetation communities due to similar geology, topography, and climate (ECOMAP 1993). Therefore, differences in vegetation between park forests and forests in the same Ecological Subsection should primarily be due to different management regimes, rather than environmental gradients or differences in climate. We used the publicly available perturbed, swapped USFS-FIA plot locations (http://www.fia.fs.fed.us/tools-data/, accessed April 2015), and included the most recent 5-year window of plot surveys that were available at the start of this study (i.e., 2009–2013). Perturbed plot locations are within a 1.6-km radius in a random direction of the true plot location (most are within 0.8 km) to conceal the true location while also ensuring the data are representative for regional analyses (McRoberts et al. 2005). The USFS-FIA program uses a three-phased sample design, where Phase 1 consists of remote sensing, Phase 2 consists of ground-based plot sampling of traditional FIA variables (e.g., tree growth and mortality) at a density of 1 plot/2428 ha, and Phase 3 plots consist of more detailed forest health surveys (e.g., herbaceous vegetation) in roughly 1/16th of Phase 2 plots (Bechtold and Patterson 2005). We included all USFS-FIA Phase 1 plots with land-cover and ownership data to characterize land use in the matrix. This included USFS-FIA plots that fell within NPS lands, to quantify the extent of forestlands that are held by different land owners and agencies, as well as the overall proportion of forests that are reserved from timber harvesting. We used the USFS-FIA designations of land cover (e.g., forest, non-forest, developed), ownership type, and reserved status that were recorded for each plot for the matrix characterization. For further details on USFS-FIA plot design and definitions of land-cover and ownership status, see US Forest Service (2015*b*).

For each park, we calculated the percent of the matrix that was forested as the percent of the FIA plot areas that could be forested (e.g., excluding large waterbodies) using USFS-FIA's classifications of plot areas by land cover. Forest land was defined as land that is stocked at least 10% by forest trees of any size, or land that was formerly at least 10% stocked by tree cover and not currently developed for a non-forest use (Bechtold and Patterson 2005). Natural land covers that could not support forest, such as waterbodies, emergent wetlands, and sand beaches, were excluded from the calculation. We calculated proportion of forestland by ownership and reserved status by summing USFS-FIA's classifications of land cover and ownership by forested area within each plot across all USFS-FIA plots in the Ecological Subsection(s). Reserved forestlands are those where timber harvesting is prohibited, typically by law (US Forest Service 2015*b*).

Metric calculations

To characterize matrix forests, we used USFS-FIA Phase 2 plots with at least one recorded and sampled forest condition to estimate tree growth and mortality rates and all structural metrics except CWD. This included plots that were partially non-forest, but we only included data from the forested part of each plot in the metric calculations. USFS-FIA plots that fell within parks were not included in the USFS-FIA sample for metric calculations, because we wanted to explicitly compare the forest structure of protected park forests with non-park (i.e., matrix) forests. USFS-FIA Phase 3 plots were used to calculate CWD volume. To characterize forests in each park, we included all forest plots, which are roughly equivalent to FIA Phase 3 plots, within each park that are actively monitored by NPS I&M. We calculated metrics of forest structure, along with tree growth and mortality rates, using the same methods across NPS I&M and USFS-FIA plot data. Because NPS I&M protocols were adapted from the USFS-FIA protocols, only minor adjustments, such as standardizing by unit of area, were required for data in this study to be comparable across programs and sites. For each metric calculation, we denote where adjustments were required, such as increasing the minimum tree DBH from NPS plots (10 cm) to match USFS-FIA's minimum tree DBH (12.7 cm). For structural stage, we classified plots as pole, mature, late succession, and mosaic (designated for plots

Table 2. Land-cover and ownership patterns for each park matrix.

				Forest by ownership		
Network	Park	% Forested matrix	% Reserved	% Private	% Federal	% State/Local
ERMN	ALPO	73.63	3.68	73.05	7.35	19.60
	BLUE	63.71	3.41	80.26	11.58	8.15
	DEWA	75.02	6.77	76.39	4.68	18.93
	FONE	72.69	3.61	77.31	10.10	12.59
	FRHI	60.33	1.76	86.56	1.34	12.10
	GARI	83.45	0.51	97.24	1.30	1.47
	JOFL	72.69	3.61	77.31	10.10	12.59
	NERI	84.13	1.68	92.51	5.93	1.56
GLKN	APIS	77.18	8.83	62.74	9.78	27.49
	GRPO	93.78	19.20	25.29	43.37	31.34
	INDU	29.50	10.55	69.98	2.59	27.43
	ISRO	89.20	7.85	36.15	25.33	38.52
	MISS	34.03	6.38	85.19	3.34	11.47
	PIRO	95.93	4.35	43.85	33.43	22.72
	SACN	68.90	2.88	54.84	12.59	32.57
	SLBE	60.85	7.99	60.66	20.98	18.35
	VOYA	94.11	15.99	23.94	33.20	42.86
MIDN	APCO	65.53	0.08	95.69	0.08	4.23
	BOWA	65.53	0.08	95.69	0.08	4.23
	FRSP	60.55	0.70	94.04	1.77	4.19
	GETT	23.38	9.10	73.59	1.08	25.34
	HOFU	23.38	9.10	73.59	1.08	25.34
	PETE	59.28	0.83	93.52	2.20	4.27
	RICH	60.13	1.17	94.37	2.00	3.64
	SHEN	82.60	19.00	54.94	38.25	6.81
	VAFO	22.54	12.96	73.46	0.54	26.00
NCBN	CACO	47.81	16.24	50.31	17.31	32.39
	COLO	57.76	5.84	87.87	8.20	3.92
	GEWA	51.09	21.29	66.36	28.77	4.87
	SAHI	23.57	25.96	29.46	9.53	61.01
	THST	37.73	12.77	72.08	6.98	20.94
NCRN	ANTI	31.04	1.41	83.25	11.17	5.59
	CATO	82.60	19.00	54.94	38.25	6.81
	CHOH	51.07	6.17	70.27	9.87	19.87
	GWMP	29.25	14.86	73.65	3.96	22.39
	HAFE	52.18	10.99	67.66	26.50	5.84
	MANA	38.52	14.59	76.46	6.08	17.46
	MONO	38.52	14.59	76.46	6.08	17.46
	NACE	37.73	12.77	72.08	6.98	20.94
	PRWI	56.72	1.39	91.76	2.62	5.62
	ROCR	27.14	14.95	72.74	3.27	23.99
	WOTR	38.52	14.59	76.46	6.08	17.46
NETN	ACAD	87.00	6.81	87.63	6.81	5.56
	MABI	75.01	3.26	90.11	2.71	7.18
	MIMA	60.38	3.25	73.52	2.88	23.60
	MORR	25.34	10.25	73.54	1.66	24.80
	ROVA	47.55	8.48	84.75	1.17	14.08
	SAGA	75.01	3.26	90.11	2.71	7.18
	SARA	39.29	2.95	88.23	0.00	11.77
	WEFA	60.46	11.17	64.05	2.87	33.08

Notes: % Forested matrix is the percent of the matrix that is forested. % Reserved is the percent of forest that is reserved from timber production. Forest by ownership is the percent of forest in various ownership categories.

that did not fit into any of the previous categories) following a slightly modified version of the structural stage metric developed for the Northeast Temperate Network's (NETN) Ecological Integrity Scorecard (Tierney et al. 2015). This metric uses relative basal area by size classes to classify plots into each stage. To make the structural stage classifications comparable across NPS I&M and USFS-FIA, we changed the minimum size in the smallest size class to be 12.7 cm DBH, instead of 10 cm DBH (the NETN's cutoff), because 12.7 cm is USFS-FIA's minimum DBH for trees. The structural stage classification only includes live canopy trees (i.e., dominant, codominant, and intermediate crown classes) to calculate relative basal area by size class, and I&M networks and/or parks that did not classify trees by crown class were not included in this metric. Ten parks were not included in the structural stage classification because of this protocol difference, and this included all Great Lakes Network (GLKN) parks and Cape Cod NS (CACO). However, we did classify structural stage for the USFS-FIA plots in the matrix paired with these parks to characterize forests in the surrounding matrix.

Live tree basal area for each plot was calculated by summing the basal area for all live trees ≥ 12.7 cm DBH within a plot. Because plot sizes vary across NPS I&M networks and across FIA plots, we converted basal area on the plot to m^2/ha using only the area of the plot that was classified as a sampled forest condition. Live tree density overall and by size class also included all live trees ≥ 12.7 cm DBH and was converted to number of stems/ha. Dead tree basal area was the sum of the basal area of all dead standing trees (snags) that were < 45° from vertical and ≥ 12.7 cm DBH and was converted to m^2/ha. Likewise, snag density overall and by size class included all standing dead trees that were < 45° from vertical and ≥ 12.7 cm DBH. Trees that were leaning ≥ 45° from vertical were classified as CWD and were not included in the dead tree basal area or snag density calculation. The methods for calculating CWD volume followed those detailed in Tierney et al. (2015), with one minor adjustment. To match USFS-FIA methods, the minimum diameter for a CWD piece with a decay class of 5 was 12.7 cm diameter. For decay classes 1–4, the minimum CWD diameter was 10 cm. For all pieces, the minimum length was 1 m, while also maintaining the minimum diameter. CWD is not sampled as part of CACO's forest monitoring program, so was not included in this analysis.

Tree growth and mortality rates required repeated surveys of plots, along with tracking of individual tree status (i.e., live or dead) and growth. Networks or parks that did not meet these requirements were not included in these metrics, although we calculated growth and mortality rates for each park's corresponding matrix using USFS-FIA plots. Growth and mortality rates were not available for the nine GLKN parks and Cape Cod NS (CACO) due to protocol differences. Colonial NHP (COLO) growth and mortality rates were not available because only one survey has been conducted in this park at the time of this analysis. We used percentage of basal area/year of trees ≥ 12.7 cm DBH to represent tree growth because it standardized growth relative to initial tree basal area (Dobbertin 2005), and included only canopy trees (e.g., dominant, codominant, or intermediate crown class) to remove the influence of subcanopy trees with suppressed growth rates. We calculated tree growth rate by taking the difference in consecutive DBH measurements on individual trees that were alive over two surveys, calculating percent change in basal area, and converting this to an annual rate for each tree. We then averaged the percentage of basal area growth rate for individual trees across the plot. Tree mortality rate was calculated from repeated surveys on each plot as the percent of canopy trees that died during the interval between surveys and converted to an annual basis. We did not include trees that were harvested between surveys in the mortality rate calculation.

Data analysis

We used R 3.2.0 for all statistical analyses (R Core Team 2015). For comparisons between parks and matrix forests, each park was individually compared to its corresponding matrix using the USFS-FIA plots in the same Ecological Subsection as the park. The nature of the data distributions (e.g., overdispersed count data) in our combined USFS-FIA and NPS I&M data set prevented us from using parametric methods to test for mean differences in forest metrics between a park and its surrounding matrix, including unequal variance and sample size between USFS-FIA and NPS I&M, increasing variance with USFS-FIA plot size, different plot areas, and greatly skewed error distributions as indicated by residual plots. We controlled for differences in plot areas by standardizing all metrics to a per hectare basis prior to analysis. To test for differences in the metrics between plots in each USFS-FIA and NPS I&M grouping, we used the permTS function in R's perm package (Fay and Shaw 2010) to perform two-sided, two-sample permutation tests (Gotelli and Ellison 2012). PermTS is a nonparametric test that performs many iterations of randomly shuffled group membership (i.e., USFS-FIA or NPS I&M) of plots while maintaining the original sample size of each group, and calculates the difference in means between both groups. The observed mean difference between NPS I&M and USFS-FIA is then compared with the distribution of means calculated from the permutations to calculate a *P*-value. To account for multiple comparisons, we calculated q-values within each metric using the q-value package in R (Dabney and Storey 2015). The q-value approach reduces the chance of a Type I error based on the number of tests with significant *P*-values and has more power than other common multiple comparison corrections, such as Bonferroni correction (Roback and Askins 2005). We considered a q-value ≤0.05 to indicate a significant difference in the mean of a metric between a park (NPS I&M) and the surrounding matrix (USFS-FIA).

Area of NPS I&M plots did not vary within a park, but did vary across networks. The area of forest varied in USFS-FIA plots. To account

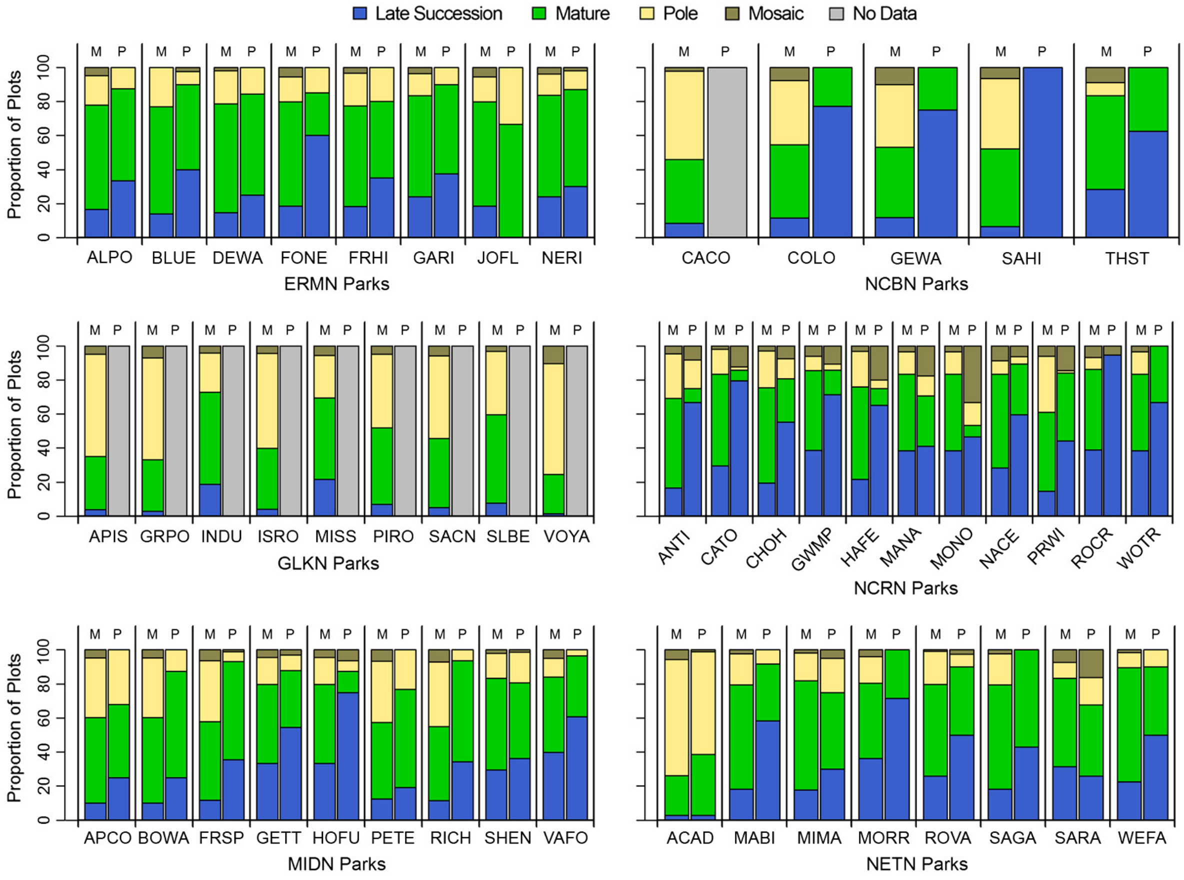

Fig. 2. Proportion of plots by structural stage in USFS-FIA plots in the surrounding matrix (M) and NPS I&M plots in parks (P). Parks where this metric could not be calculated are represented by gray bars.

for differences in plot areas, we converted NPS I&M and USFS-FIA data to standard units (e.g., density of live trees per hectare). For graphical comparisons between NPS I&M parks and their corresponding matrix, we calculated weighted averages and weighted standard errors by metric and by group (NPS I&M and USFS-FIA), with plot area as the weight.

Results

Matrix characteristics

Parks varied in the proportion of the surrounding matrix that was forested, from as high as 95% for Pictured Rocks NL (PIRO) to as low as 22% forested for Valley Forge NHP (VAFO; Table 2). Parks in the National Capital Region Network (NCRN) tended to have the lowest proportion of forest land cover in the surrounding matrix, whereas parks in the GLKN tended to have the greatest proportion of forest land cover in the matrix. For the majority of parks outside of the GLKN, forests in the surrounding matrix were largely under private ownership. In GLKN, USFS and state/local agencies comprised the majority of matrix forest ownership, particularly for Grand Portage National Monument (GRPO; NMo), ISRO, PIRO, and VOYA. Outside of GLKN, state/local agencies tended to hold the next largest percent of forest matrix after private landowners. For all parks, only a small proportion of matrix forests were reserved from timber production, indicating that the protection status of parks is unique in the region (Table 2).

Structural metrics

Forest plots in the surrounding matrix were primarily classified as pole or mature, and in nearly every case, parks had a greater proportion of plots classified as late succession (Fig. 2). Live tree basal area averaged 33% greater in parks than the surrounding forest matrix (Fig. 3). Density of live trees ≥ 30 cm DBH was

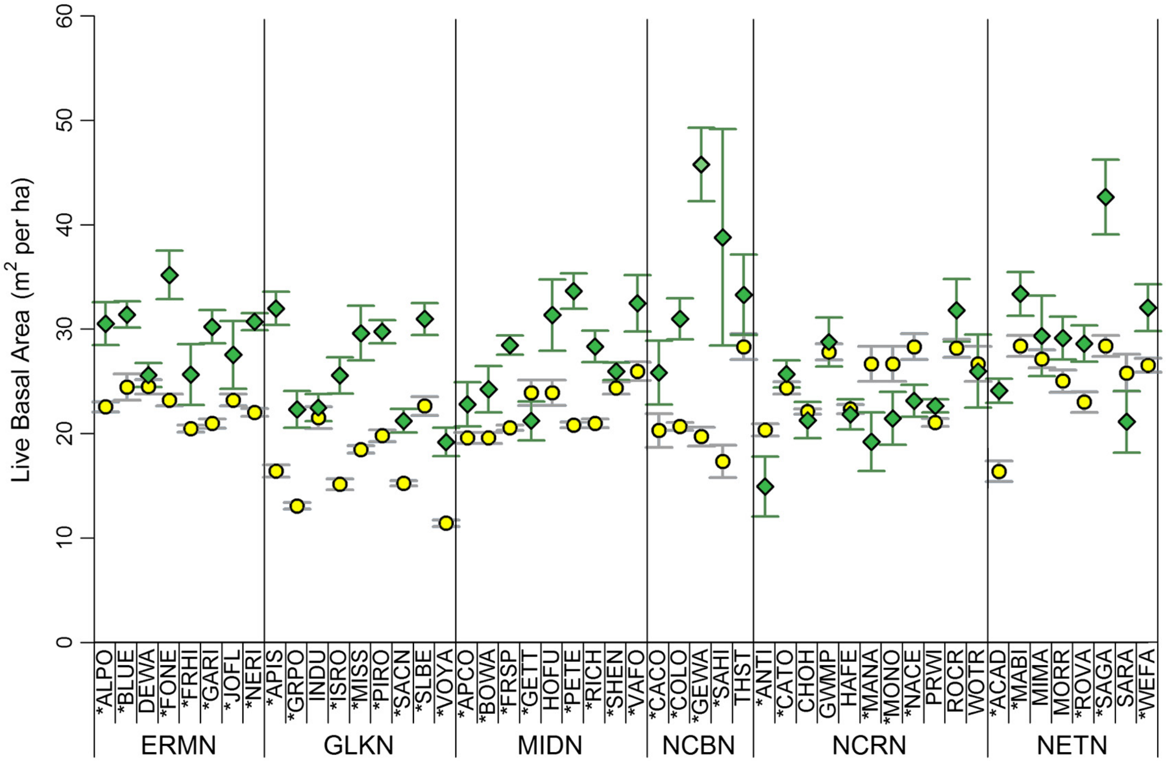

Fig. 3. Mean live tree basal area (m²/ha) and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). Asterisks indicate q-values ≤ 0.05.

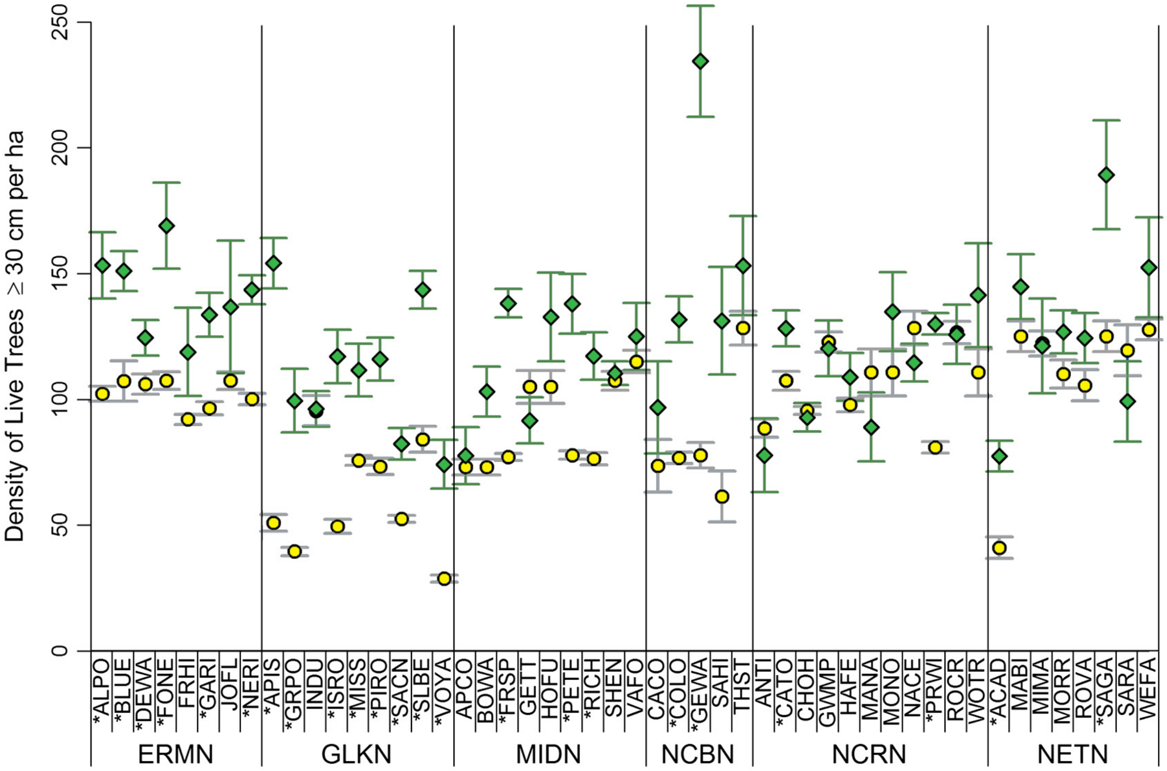

Fig. 4. Mean density of live trees ≥ 30 cm DBH (number of stems/ha) and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). Asterisks indicate q-values ≤ 0.05.

greater in park forests than matrix forests for all but six parks, with parks averaging 46% greater density of live trees ≥ 30 cm DBH than matrix forests (Fig. 4). Density of live trees ≥ 30 cm DBH was lowest in the matrix forests in the northern parts of this study, including parks in GLKN and Acadia NP (ACAD) in NETN. However, density of live trees ≥ 30 cm DBH in GLKN parks was similar to densities of other parks in the study. Density of live trees ≥ 60 cm DBH was greater in all but six parks, with parks averaging 81% greater densities than matrix forests (Fig. 5). While Eastern Rivers and Mountains Network (ERMN) and GLKN parks had comparatively low densities of trees ≥ 60 cm DBH relative to other parks in the study, densities tended to be greater in parks than in parks' corresponding matrix.

Differences between parks and matrix forests were less extreme for snags, although these metrics followed similar patterns as live tree metrics. Parks tended to have greater dead tree basal area (Fig. 6), particularly in the ERMN and the GLKN parks. While only four parks (Apostle Islands NL [APIS], GRPO, ISRO, and Catoctin Mountain Park [CATO]) had a significantly greater density of large-diameter (≥ 30 cm DBH) snags, large-diameter snags consistently trended more abundant in parks than matrix forests (Fig. 7). CWD volume was considerably greater in most parks, averaging more than twice the amount (135% greater) found in matrix forests (Fig. 8). Only two of the 50 parks in this study (Johnstown Flood National Memorial [JOFL] and Minute Man NHS [MIMA]) had lower average CWD volume than surrounding matrix forests.

Tree growth and mortality

Tree growth rates, represented as percentage of basal area growth/year, were consistently lower in park forests than surrounding matrix forests (Fig. 9). Growth rates of park forests were roughly half of matrix forest growth rates, and most parks were significantly different than

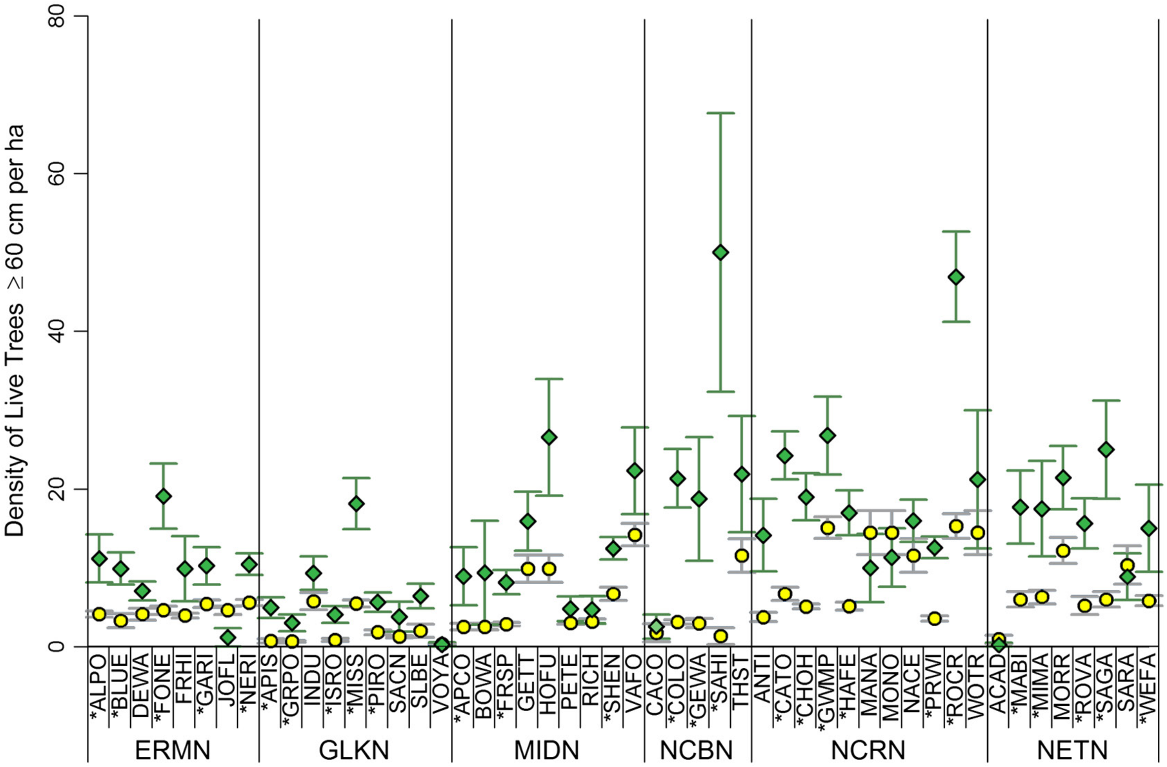

Fig. 5. Mean density of live trees ≥ 60 cm DBH (number of stems/ha) and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). Asterisks indicate q-values ≤ 0.05.

the matrix forests. While not as distinct, the annual tree mortality rates tended to be lower in park forests than in surrounding matrix forests (Fig. 10). The largest mortality rate observed in a park was in Sagamore Hill NHS (SAHI), which only has four NPS forest plots, and could be overly influenced by mortality of a few trees. Mortality rates based on at least 10 plots, which most of the parks in this study have, tend to be more robust.

Discussion

Park vs. matrix forests

Results of this study indicate that the majority of forests in national parks across the eastern United States are distinct from their surrounding matrix in forest structure and dynamics, and represent complex forest structure typical of older forest habitat. Overall, park forests tended to have a greater proportion of late-successional forest, greater live tree basal area, greater densities of live and dead large trees, and considerably larger volume of CWD. Live tree basal area in 22 parks has even exceeded levels typical for eastern old-growth forests, which average 29 m^2/ha (range: 23–40 m^2/ha; Keddy and Drummond 1996). In contrast, there were no matrix forests that averaged more than 29 m^2/ha. Differences in tree growth and mortality rates between park and matrix forests suggest that forest dynamics are different between park and matrix forests, which may also be due to parks having older forests than in the matrix. For example, Larson et al. (2015) found greater percent annual mortality in young even-aged forests (4.2%) than old-growth forests (0.6%) in the northwestern United States due primarily to density-dependent competition for light in younger stands. Busing (2005) found annual mortality rates in southeastern old-growth cove forests to range from 0.5% to 1.4% among stands. In our study, forests in 20 parks had mortality rates below 1.4%, whereas only five of the surrounding matrix forests paired with parks had mortality rates below 1.4%.

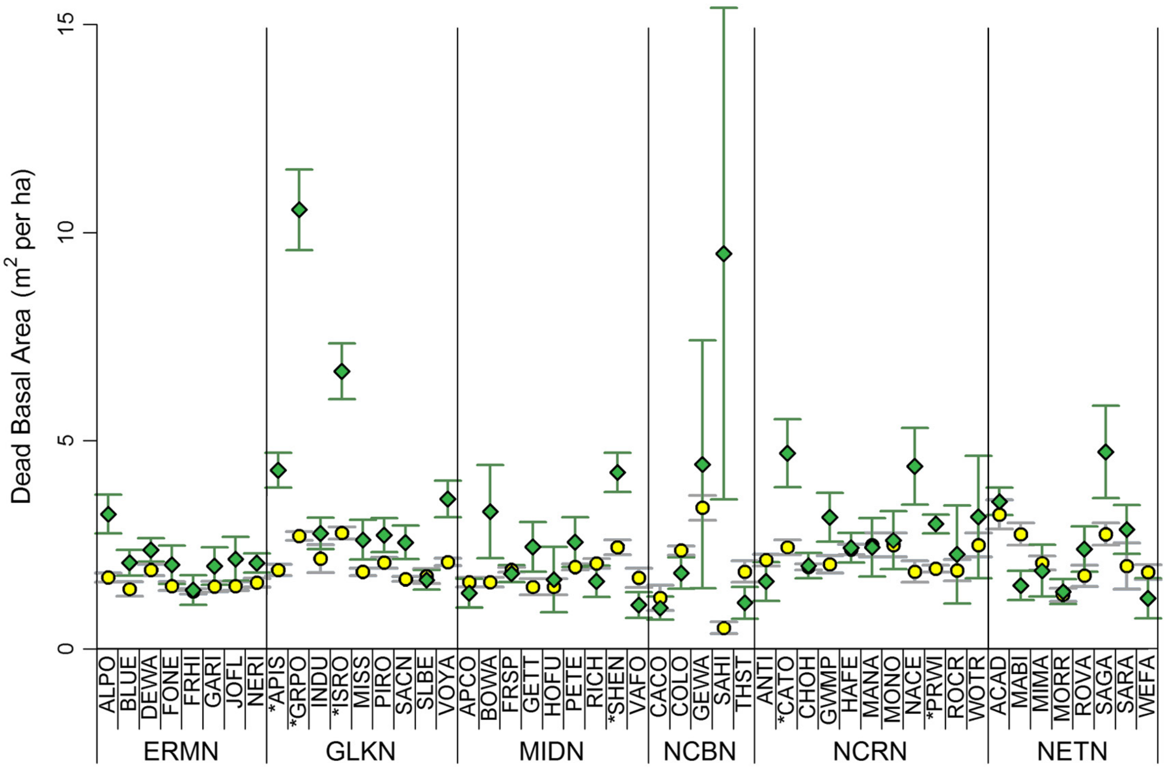

Fig. 6. Mean dead tree basal area (m^2/ha) and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). Asterisks indicate q-values ≤ 0.05.

The different structural patterns we observed between matrix and park forests were similar to those found in studies that compared managed and old-growth forests. Compared with managed forests, old-growth forests have considerably more CWD volume (Duvall and Grigal 1999, Siitonen 2001), greater live and dead tree basal area (McGee et al. 1999, Silver et al. 2013), and greater density of large-diameter (≥ 30 cm DBH) live and dead trees (Goodburn and Lorimer 1998, Hale et al. 1999). However, the differences between park and matrix forests in our study were often less pronounced than those found in comparisons between old-growth and managed forests, particularly for dead wood. For example, CWD volume in old-growth forests in the eastern United States has been found to range from 66 m^3/ha to over 140 m^3/ha (Muller and Liu 1991, Goodburn and Lorimer 1998), whereas all but seven parks averaged less than 60 m^3/ha of CWD. Additionally, Goodburn and Lorimer (1998) found that old-growth forests averaged more than double the density of large-diameter snags (25–40 snags/ha) compared with selectively managed mature forests (12 snags/ha), whereas most parks only had about 20% greater densities of large snags than matrix forests. Old-growth structure can take centuries to develop and may not be achievable in managed forests (Spies and Turner 1999). Given that prior to their establishment, park forests in the eastern United States often shared similar land-use histories with surrounding lands (e.g., logging, land clearing for agriculture), the second-growth forests that largely comprise park forests may be a more realistic baseline to compare with matrix forests managed for timber. The next steps are to determine whether park forests have enough older forest structure to support species dependent on this structure, and to determine minimum requirements to support these species.

Several battlefield parks, including GETT, MANA, MIMA, Monocacy NB (MONO), and SARA, did not have older forest structure compared with surrounding forests. For example, most of these parks did not have greater live tree

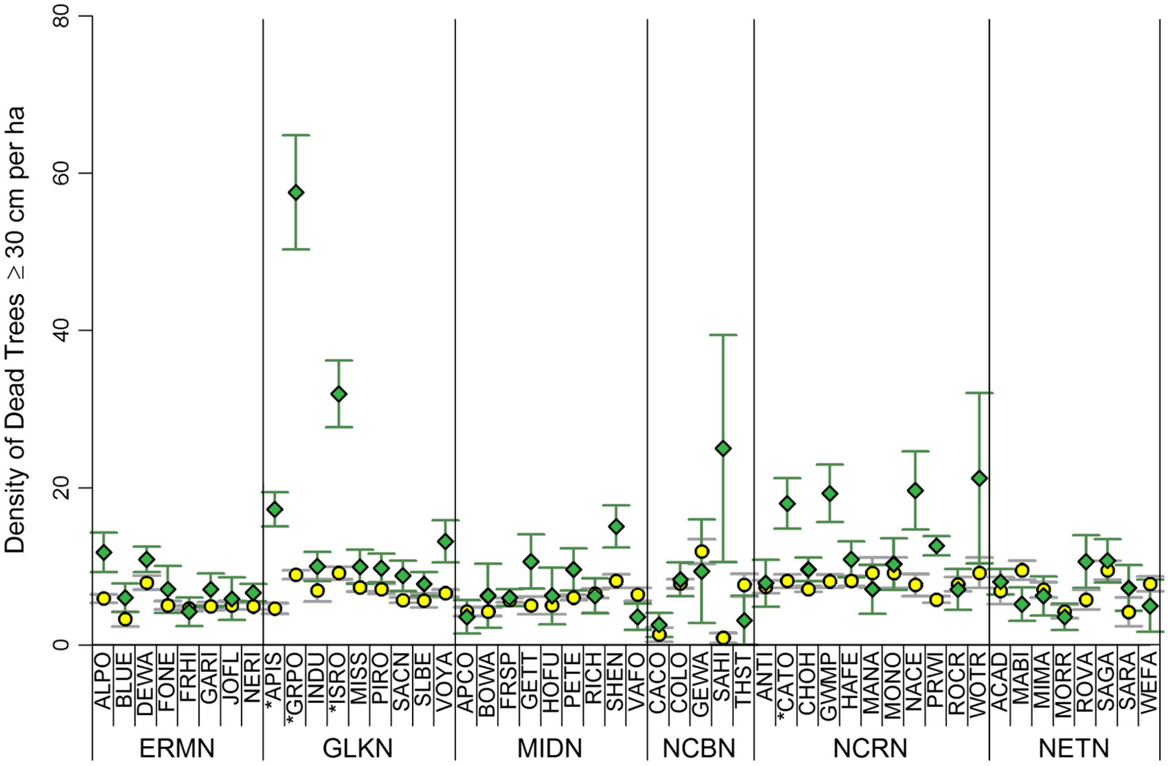

Fig. 7. Mean density of dead trees ≥ 30 cm DBH (number of stems/ha) and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). Asterisks indicate q-values ≤ 0.05.

basal area or a greater density of large-diameter trees. The forests in these battlefield parks tend to occur in small patches and include areas where old fields are transitioning to forest, and this at least partially explains the lack of older forest structure compared with matrix forests. Over time, we expect forests in these battlefield parks to develop older forest structure.

Based on a review of species dependent on dead wood in European temperate and boreal forests, Müller and Bütler (2010) suggested a minimum of 20–50 m^3/ha of CWD volume was required to sustain a broad range of dead wood-dependent taxa. Comparing this threshold to average CWD volume in park and matrix forests, 90% of the parks in this study exceeded 20 m^3/ha of CWD volume and 30% of parks exceeded 50 m^3/ha of CWD volume. In contrast, only 12% of matrix forests exceeded 20 m^3/ha, and no matrix forests exceeded 50 m^3/ha of CWD.

Work by Guénette and Villard (2005) estimated that a minimum density of 80 stems/ha of large-diameter (≥ 30 cm DBH) trees was required to support a broad range of late-seral bird species. A similar study on brown creeper (*Certhis americana*) habitat requirements suggested a minimum density of 127 stems/ha of large-diameter trees (Poulin et al. 2008). In our study, 92% of parks had an average density that met the minimum density of 80 large-diameter trees/ha for late-seral bird species, and 44% of park forests met the greater density requirement of 127 large-diameter trees/ha for brown creepers. In contrast, average density in only 66% of matrix forests met the density requirements for late-seral bird species and only 6% of matrix forests met the greater density requirement for brown creepers. Although these results suggest that the structure of park forests may be sufficient to support many species dependent on dead wood and large trees, important structural components that are slow to develop in forests may still be lacking in parks, such as the large-diameter down-logs required by American martens (*Martes americana*) for den and resting sites (Chapin et al. 1997).

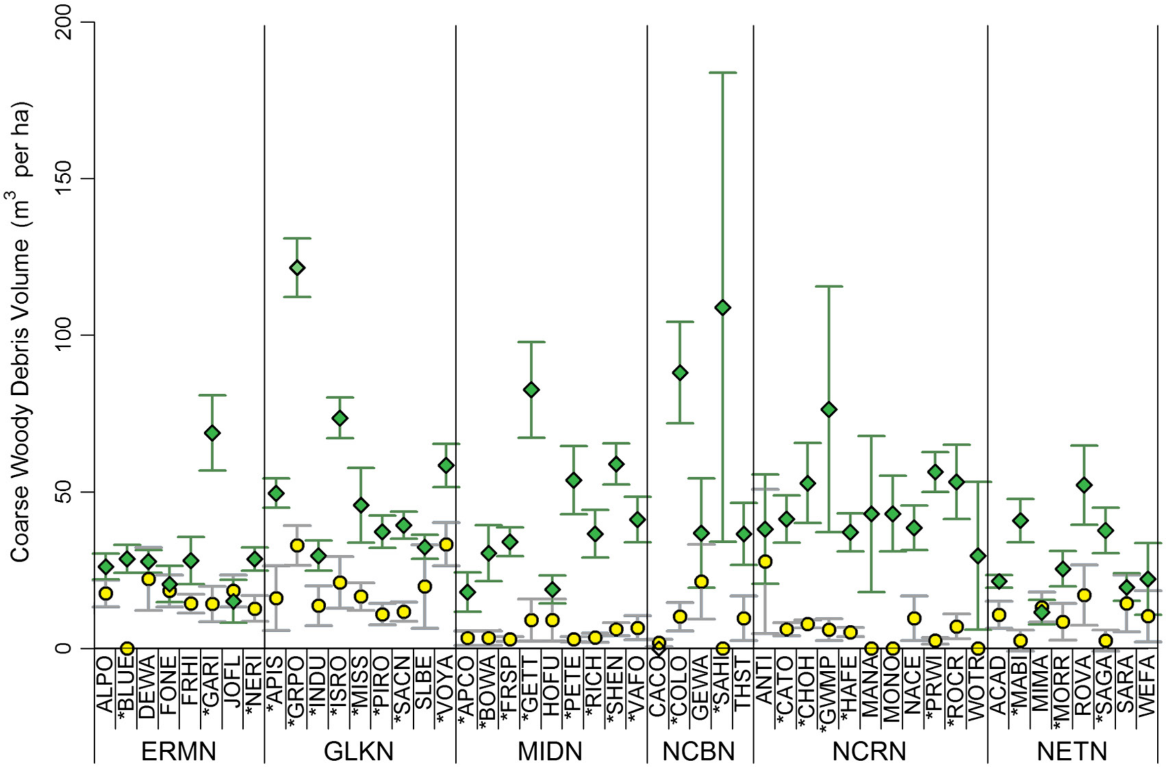

Fig. 8. Mean volume of coarse woody debris and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). An open diamond indicates that data were unavailable for a park (CACO). Asterisks indicate q-values ≤ 0.05.

While the thresholds we presented for large-diameter trees and CWD volume may not be directly applicable to all of the forest types in this study, they at least suggest that the differences between park and matrix forests are ecologically significant. Additionally, guidelines such as those presented in Müller and Bütler (2010) are lacking for eastern US forests, particularly for the oak/hickory forests common in the southern part of this study. Many of the I&M networks that are monitoring park forests also monitor breeding landbirds (e.g., ERMN, GLKN, MIDN, NETN, and NCRN), providing a unique opportunity for future research to examine how forest structure influences bird communities in parks, and to assess whether forest structure in parks is adequate to support bird species dependent on older forests.

An important caveat for the CWD volume metric relates to sample size in the USFS-FIA data. Tree density and basal area metrics, which occur in Phase 2 USFS-FIA plots, typically included several hundred to thousands of USFS-FIA plots per forest matrix for this analysis. In contrast, CWD has traditionally only been measured on Phase 3 USFS-FIA plots, and some matrix forests had as few as three Phase 3 plots to represent matrix forests (Appendix S1: Table S1). USFS-FIA has recently started collecting CWD data in Phase 2 plots (US Forest Service 2015*b*), and this will greatly improve the ability to estimate levels of CWD on the landscape. Small sample size in a few parks (e.g., Booker T. Washington NMo [BOWA], George Washington Birthplace NMo [GEWA], Sagamore Hill NHS [SAHI], Thomas Stone NHS [THST], and Wolf Trap Park for the Performing Arts [WOTR]) may have resulted in low power to detect differences between these parks and matrix forests for CWD and other metrics. These parks also tended to have fairly wide error bars across the metrics due to high variability and small sample size.

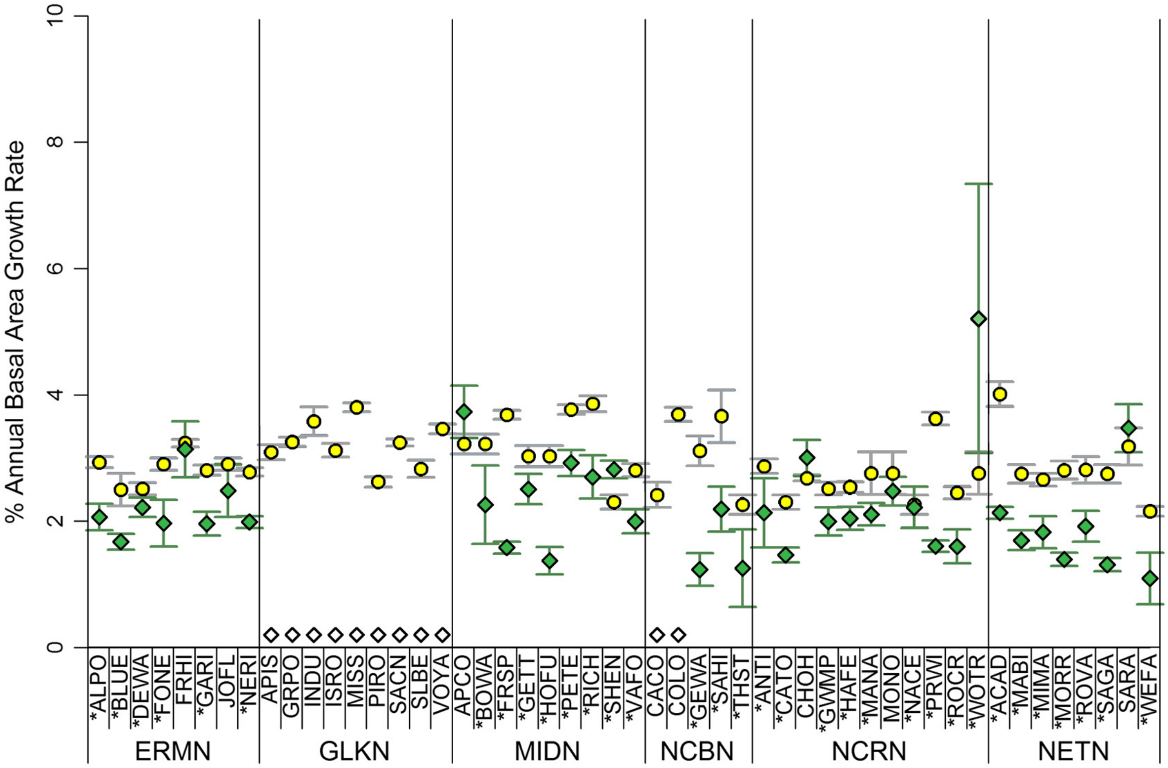

Fig. 9. Mean annual growth rate (% Basal Area) and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). Open diamonds indicate that data were unavailable for a given park. Asterisks indicate q-values ≤ 0.05.

Management recommendations

Based on the results of this study, we propose several important management recommendations. First, given that park forests harbor structural features (e.g., large trees and large CWD volume) that are otherwise deficient on the landscape, their continued protection and development are valuable beyond the boundaries of the park. Park forests also represent some of the few areas in the eastern United States that are largely under natural disturbance regimes. This offers a unique opportunity to track long-term forest development and natural processes in the absence of timber harvesting over a range of forest types in the region. We therefore recommend that park managers continue to allow for natural disturbances and the development of older structure in park forests despite potential outside pressure from the public or other park decision-makers to "clean up" the forest after disturbances such as windthrow or ice storms. Second, long-term maintenance of regional biodiversity, particularly related to species dependent on older forest habitat, will require changes in how matrix forests are managed. Throughout the study area, matrix forests lacked the minimum requirements for dead wood and large trees to maintain species dependent on this structure, whereas parks often exceeded the minimum requirements. Long-term maintenance of regional biodiversity will likely require increases in older forest structure in the matrix. This is particularly true for the northern Great Lakes region. Despite having the greatest proportions of forest in the surrounding matrix, the matrix forests for GRPO, ISRO, and VOYA had the lowest densities of live trees ≥ 30 cm DBH, and CWD volume and large snag densities were considerably lower in the matrix forests than the corresponding parks. We encourage park staff to include the widespread need to increase older forest structure across the region in their outreach to the public and stakeholders, and

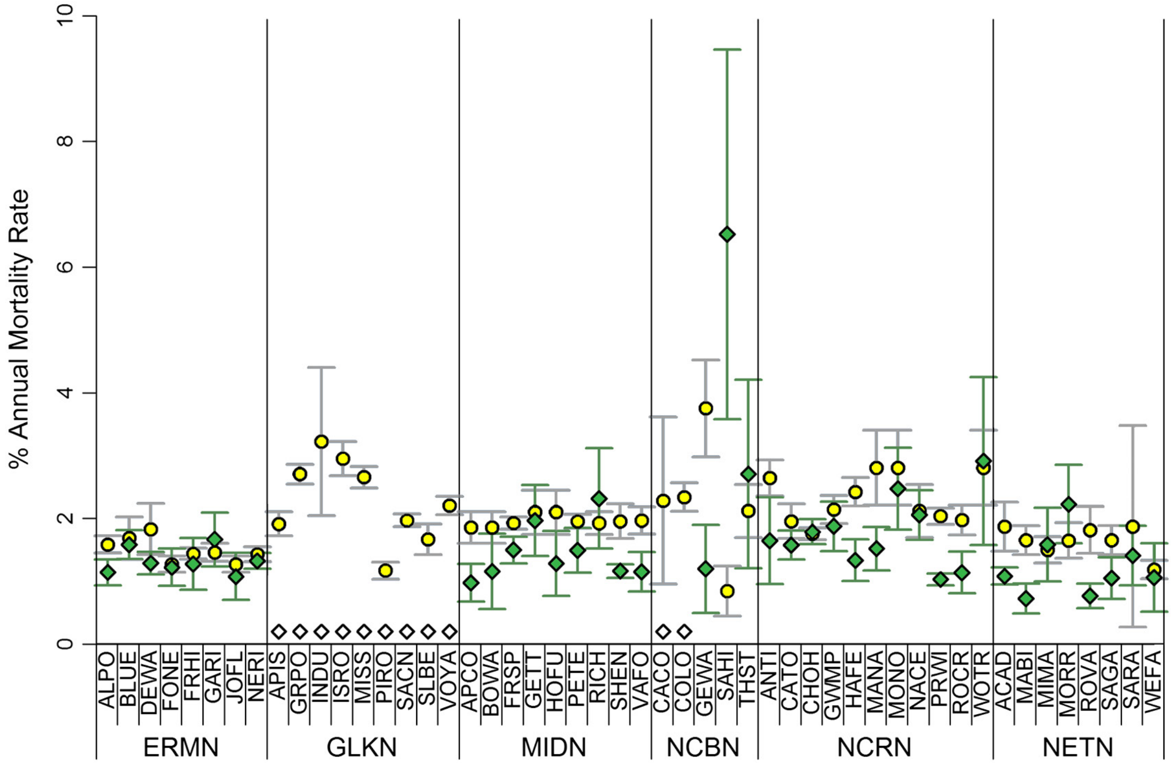

Fig. 10. Mean annual mortality rate and ±1 SE by NPS unit (green diamonds) and the surrounding matrix (yellow circles). Open diamonds indicate that data were unavailable for a park. There were no significant differences between park and matrix forests.

to work with local landowners and nearby state and federal land managers to increase older forest structure and connectivity of matrix forests.

In *Revisiting Leopold: Resource Stewardship in National Parks*, the NPS proposed that national parks be leaders in conservation by protecting core sites of biodiversity and ecological processes (Colwell et al. 2012). The results of our study are consistent with this objective, as eastern parks provide core sites of older forest structure that are otherwise deficient on the landscape. In *Revisiting Leopold*, NPS also recognized that parks are part of a larger landscape and that ecosystem health and connectivity across the matrix are essential for ecosystem resilience and maintenance of biodiversity in parks (Colwell et al. 2012). Our results underscore the need to take larger regional approaches to resource management. As the NPS moves into its next century of land preservation, we encourage managers to consider parks an important component of a larger regional effort to preserve biodiversity and ecosystem processes. The data collected by the NPS I&M programs will continue to provide important information and guidance toward these regional conservation efforts.

CONCLUSIONS

Overall results of this study indicate that regardless of size or type of park, forests in national parks across the eastern United States are distinct from their surrounding matrix and represent regionally significant areas of forest structure characteristic of older forests. Our study is the first to compare forest structure in protected lands with the surrounding forest matrix over such a large area of the United States and is only possible because of the 10+ years of data that are now publicly available from USFS-FIA and NPS I&M. As eastern forests respond to climate change and other stressors, the trends captured by long-term monitoring in eastern national parks will continue to provide valuable insights into forest dynamics and important guidance for land managers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1404/supinfo