Eastern national parks protect greater tree species diversity than unprotected matrix forests.

Authors: Kathryn M. Miller[a,b], Brian J. McGill[b], Brian R. Mitchell[c], Jim Comiskey[d], Fred W. Dieffenbach[e], Elizabeth R. Matthews[f], Stephanie J. Perles[g], John Paul Schmit[f], and Aaron S. Weed[e]

[a]National Park Service, Northeast Temperate Network, Bar Harbor, ME 04609, USA
[b]University of Maine, School of Biology and Ecology, Mitchell Center for Sustainability Solutions, Orono, ME 04469, USA
[c]National Park Service, Southeast Regional Office, Atlanta, GA 30303, USA
[d]National Park Service, Northeast Region Inventory and Monitoring Program, Fredericksburg, VA 22405, USA
[e]National Park Service, Northeast Temperate Network, Woodstock, VT 05091, USA
[f]National Park Service, National Capital Region Network, Washington, D.C. 20007, USA
[g]National Park Service, Eastern Rivers and Mountains Network, University Park, PA, 16802, USA

Corresponding author e-mail: kathryn_miller@nps.gov
Corresponding author address: P.O. Box 177, Bar Harbor, ME, 04609

Abstract

Decline in tree species diversity is a widespread trend in eastern US forests, with implications for ecosystem functions and services, biodiversity and vulnerability to climate change and other stressors. While some impacts on diversity are widespread such as forest pests, forest management practices vary across the landscape. For example, forests in US national parks are managed to promote ecological integrity, develop under natural disturbance regimes, and are largely protected from timber harvesting. In this study we compared forests in 39 eastern US national parks with surrounding matrix forests to assess whether forest protection has led to differences in tree diversity patterns in parks. We calculated multiple alpha and beta diversity metrics using tree stem data. We examined alpha diversity metrics at the scale of the 7.31 m radius subplot and for an equal number of individuals, and examined beta diversity at multiple scales. This is the first study to compare tree diversity in protected lands with the surrounding forest matrix over such a large area of the US, and is only possible because of the 10+ years of data that are publicly available from US Forest Service (USFS) Forest Inventory and Analysis (FIA) and the National Park Service (NPS) Inventory and Monitoring (I&M) programs. Overall, results indicated that park forests have consistently greater alpha diversity. Park forests have higher tree species richness, particularly after the influence of the number of individuals was removed. Park forests also consistently had higher Shannon Evenness, lower McNaughton Dominance, and higher percentage of rare species. Beta diversity analyses also suggest that parks were less homogenous across sites, although results are exploratory due to differences in scale and small sample size. While a number of studies have documented higher diversity in protected areas, few studies have examined multiple diversity metrics or covered the large area of our study. Combining these results with a previous study, which found parks to have consistently greater structural complexity than surrounding forests, park forests may respond differently and potentially be more resilient to climate change and other stressors than unprotected forests, as there is a greater chance that some of the tree species or size cohorts present will persist through climate change. Continued monitoring is important to determine how forests respond to climate change and other stressors, and whether specific management actions, such as protecting more forests, translocating species, or altering management practices, are necessary to maintain forest biodiversity and function.

Keywords: tree species diversity; forest management; climate change; alpha and beta diversity; Forest Inventory and Analysis; National Park Service Inventory and Monitoring

1. Introduction

Decline in tree species diversity at both local and regional scales is a widespread trend in eastern US forests (Schulte et al. 2007; Shields et al. 2007; Amatangelo et al. 2011; Nuttle et al. 2013; Thompson et al. 2013). Introductions of exotic pests and pathogens have resulted in direct loss of multiple tree species once common to the eastern forest, including American chestnut (*Castanea dentata*) and American elm (*Ulmus americana*) (Ellison et al. 2005; Loo 2009). More recently, hemlock woolly adelgid (*Adelges tsugae*) has caused widespread decline and mortality of eastern hemlock (*Tsuga canadensis*) throughout much of its range (Vose et al. 2013). Additionally, emerald ash borer (*Agrilus planipennis*) is causing extensive mortality of ash species (*Fraxinus* spp.), functionally removing ash as a component of eastern forests within the continually expanding range of infestation (Flower et al. 2013).

Tree diversity has also been impacted by an overabundance of deer throughout the eastern US (Matonis et al. 2011; Nuttle et al. 2013; Côte et al. 2014). In the Great Lakes region, elevated deer browse pressure has severely impacted conifer regeneration, particularly for northern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*) and eastern white pine (*Pinus strobus*), leading to a loss of conifer species in the canopy and increased homogeneity in regional forest composition (Rooney and Waller 2003; Côte et al. 2004; Salk et al. 2011; White 2012). Reduced tree diversity has also been documented in the mid-Atlantic and Midwest regions, where forests once dominated by multiple species of oak (*Quercus* spp.) and hickory (*Carya* spp.) are being replaced primarily by American beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) (Nowacki and Abrams 2008; Nuttle et al. 2013). Termed 'mesophication', this pattern is widespread, with the combined impacts of fire suppression, deer overabundance, altered disturbance regimes and climate change considered the likely causes (Nowacki and Abrams 2008; McEwan et al. 2011; Brose et al. 2013).

In eastern forests, such as oak-hickory and northern hardwood forests, stand-replacing disturbances are infrequent natural disturbances, with the composition in these forests driven more by frequent low intensity disturbances, environmental gradients and climate under natural conditions (Lorimer and White 2003). However, historic patterns of land use and timber harvesting have led to local and regional declines in tree species diversity (Boucher et al. 2009; Thompson et al. 2013; Kern et al. 2017). Through centuries of land clearing and timber harvesting, northeastern forest composition has become more similar across the region, less coupled with climatic factors and environmental gradients, and more dominated by early to mid-successional species (Thompson et al. 2013). These patterns have been documented in similar forest communities in the Great Lakes region (Schulte et al. 2007; Hanberry et al. 2012). Modern-day harvesting practices can also contribute to patterns of tree diversity (Neuendorff et al. 2007; Shields et al. 2007; Boucher et al. 2009; Clark and Covey 2012). For example, selection methods in northern hardwood forests have favored sugar maple (*Acer saccharum*) or American beech (*Fagus grandifolia*) regeneration over species that are less tolerant of shade, are sensitive to deer browse or that require exposed mineral soil or coarse woody debris to germinate (Nuttle et al., 2013; Kern et al. 2017). This has led to an overall decrease in tree diversity, including lower species richness and greater dominance of shade tolerant species, where applied (Neuendorff et al. 2007; Shields et al. 2007; Bolton and D'Amato 2011; Kern et al. 2017). At the other extreme, even-aged management also tends to favor forests dominated by a few early successional species, such as quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera;* Schulte et al. 2005). Conversely, moderate intensity removals, such as shelterwood cutting, have been shown to maintain or enhance species diversity compared to other harvesting methods (Niese and Strong 1992).

Higher tree diversity has been associated with greater ecosystem functions and services at local (Gamfeldt et al. 2013; Lefcheck et al. 2015) and regional scales (van der Plas et al. 2016), along with greater site productivity (Paquette and Messier 2011; Vilá et al. 2013), and increased diversity of forest flora and fauna (Schmit et al. 2005; Hobson and Bayne 2000; Barbier et al. 2008; Sobek et al. 2009). Higher tree diversity can also provide greater forest resilience, which is the capacity for ecosystems to absorb disturbance and change while maintaining similar ecosystem functions, composition and structure (Elmquist et al., 2003; Millar et al., 2007). For example, higher tree diversity can reduce impacts of insect herbivory (Jactel and Brockerhoff 2007) and moderate the effects of environmental fluctuations (Aussenac et al. 2016). Moreover, in a changing climate, where species-specific responses are unknown, managing forests to promote tree diversity is a commonly suggested strategy for promoting forest resilience and adaptive capacity (Millar et al. 2007; D'Amato et al. 2011; Janowiak et al. 2014). The reasoning for this approach is that diverse forests will likely have a broader range of responses to stressors and climate change (i.e., response variability) than less diverse forests, and therefore be less vulnerable to rapid state shifts (e.g., conversion to grassland) and/or loss in ecosystem function (Millar et al. 2007). Given the importance of tree diversity, current trends of decline are of great concern to forest managers and conservationists (Schulte et al. 2007; White 2012), and understanding the underlying causes are important to ensure that eastern forests remain diverse and able to adapt to climate change and other stressors over time.

While some impacts on diversity are widespread such as forest pests and pathogens, forest management practices vary across the landscape. For example, forests in US national parks are managed to promote ecological integrity, develop under natural disturbance regimes, and are largely protected from timber harvesting. Recent meta-analyses have found protected areas to preserve greater diversity than unprotected areas (Coetzee et al. 2014; Gray et al. 2015). However these studies only considered species richness and abundance in their comparisons, and datasets from eastern US forests were underrepresented or absent in the analyses. Data available from the US Forest Service (USFS) Forest Inventory and Analysis (FIA) program have been used in a number of studies to examine patterns and drivers of tree diversity across the eastern US (Canham and Thomas 2010; Belote et al. 2011; Woodall et al. 2011; Siefert et al. 2013). However, the majority of forests monitored by USFS-FIA are not reserved from timber production (Oswalt et al. 2014; Miller et al. 2016), and forest management may have influenced the diversity patterns that were examined by these studies. The 10+ years of data available from the National Park Service (NPS) Inventory and Monitoring (I&M) program provide a unique opportunity to examine patterns of tree species diversity in forests that are managed for ecological integrity, and compare diversity patterns with unprotected forests using USFS-FIA data. Structural differences have already been documented between eastern national parks and surrounding unprotected forests, with parks consistently having greater structural complexity than surrounding forest lands (Miller et al. 2016). The observed structural differences are likely due to differences in management between parks and surrounding matrix forests. The question remains whether management differences have also influenced tree diversity patterns in park forests compared with surrounding matrix forests.

In this study we use a similar approach as Miller et al. (2016) to compare forests in eastern parks with surrounding matrix forests to assess whether the protection status of parks has led to differences in tree diversity patterns, and discuss the implications of observed patterns in the context of climate change vulnerability and adaptation. Our analysis incorporates multiple metrics of alpha and beta diversity and covers 39 national parks in the eastern US. This is the first study to compare tree diversity in protected lands with the surrounding forest matrix over such a large area of the US, and is only possible because of the 10+ years of data that are now publicly available from USFS-FIA and NPS I&M programs.

2. Methods

2.1 NPS Site Selection

The parks in this study represented a range of sizes, and included the following designations: National Battlefield (NB), National Battlefield Park (NBP), National Historical Park (NHP), National Historic Site (NHS), National Memorial (NM), National Military Park (NMP), National Monument (NMo), National Park (NP), National Recreation Area (NRA), National River (NR), and National Scenic River (NSR; Table 1). Parks were located across five NPS I&M regional networks (Figure 1) and covered

Network	Code	Park Area (ha)		# Forest Plots
		Total	Forest	
Eastern Rivers and Mountains	ERMN			
Allegheny Portage Railroad National Historic Site	ALPO	503	430	23
Bluestone National Scenic River	BLUE	1,236	1,144	40
Delaware Water Gap National Recreation Area	DEWA	22,839	19,313	96
Fort Necessity National Battlefield	FONE	373	276	20
Friendship Hill National Historic Site	FRHI	280	224	20
Gauley River National Recreation Area	GARI	1,930	1,779	40
Johnstown Flood National Memorial	JOFL	72	23	12
New River Gorge National River	NERI	21,528	19,615	102
Mid-Atlantic	MIDN			
Appomattox Court House National Historical Park	APCO	687	442	28
Booker T. Washington National Monument	BOWA	100	62	8
Fredericksburg & Spotsylvania National Military Park	FRSP	3,056	2180	104
Gettysburg National Military Park	GETT	1,743	548	33
Hopewell Furnace National Historic Site	HOFU	343	270	16
Petersburg National Battlefield	PETE	1,092	923	52
Richmond National Battlefield Park	RICH	819	585	32
Valley Forge National Historical Park	VAFO	1,395	538	28
Northeast Coastal and Barrier	NCBN			
Colonial National Historical Park	COLO	2,219	1,471	48
George Washington Birthplace National Monument	GEWA	216	87	8
Sagamore Hill National Historic Site	SAHI	29	17	4
Thomas Stone National Historic Site	THST	179	123	8
National Capital Region	NCRN			
Antietam National Battlefield	ANTI	759	129	12
Catoctin Mountain Park	CATO	2,282	2,237	49
Chesapeake and Ohio Canal National Historical Park	CHOH	5,980	4,261	75
George Washington Memorial Parkway	GWMP	1,661	969	20
Harpers Ferry National Historical Park	HAFE	1,480	1,091	20
Manassas National Battlefield Park	MANA	1,727	784	16
Monocacy National Battlefield	MONO	530	132	14
National Capital Parks East	NACE	3,088	1,942	47
Prince William Forest Park	PRWI	5,089	4,899	145
Rock Creek Park	ROCR	1,061	812	19
Wolf Trap Park for the Performing Arts	WOTR	43	26	6
Northeast Temperate	NETN			
Acadia National Park	ACAD	14,577	8,178	171
Marsh-Billings-Rockefeller National Historical Park	MABI	223	196	24
Minute Man National Historical Park	MIMA	391	234	20
Morristown National Historical Park	MORR	676	626	28
Roosevelt-Vanderbilt National Historic Sites	ROVA	446	338	40
Saint-Gaudens National Historic Site	SAGA	80	48	21
Saratoga National Historical Park	SARA	1,156	687	32
Weir Farm National Historic Site	WEFA	28	18	10

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

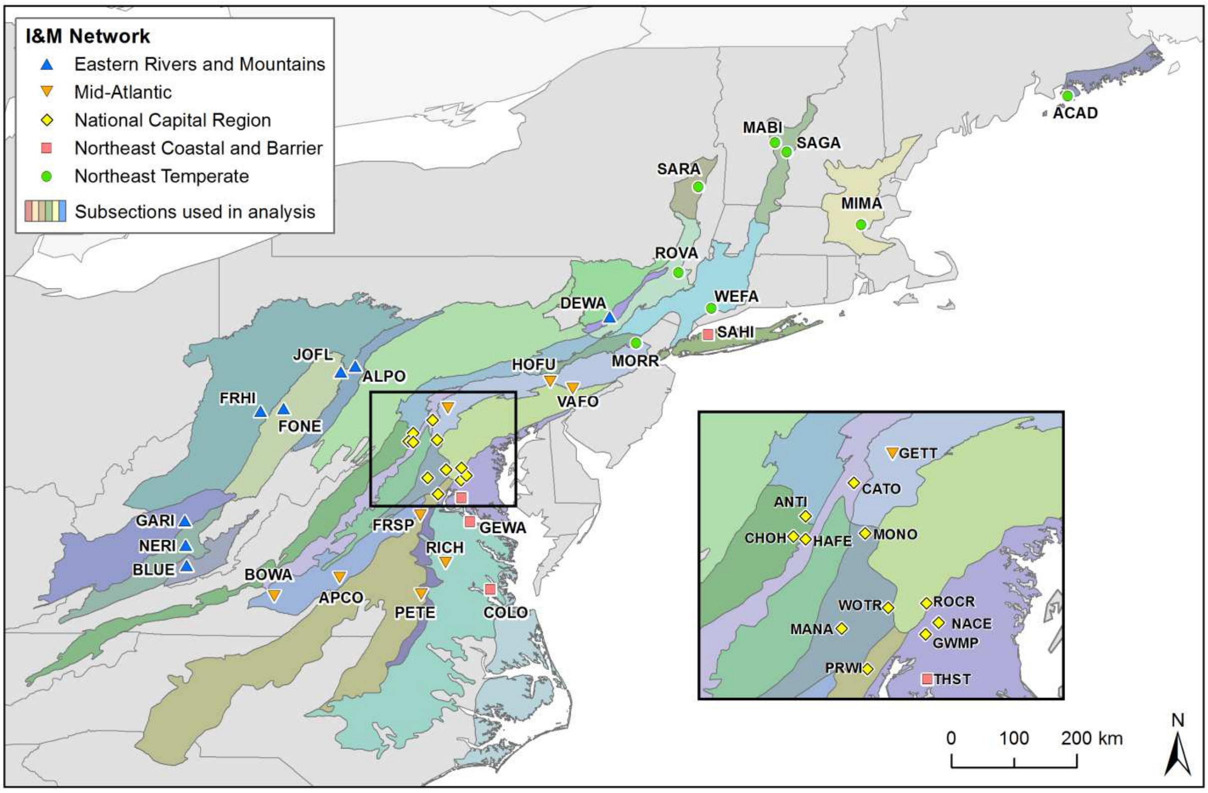

Figure 1. Map of national parks and Ecological Subsections that were included in this study. See Table 1 for full park names.

multiple forest types, including mid-Atlantic oak-hickory forests, northern hemlock-hardwood forests, and boreal spruce-fir forests. In contrast to many of the large iconic national parks in the western US, which were often set aside to protect unique environments, unusual geologic formations and/or expansive scenery, many of the parks in the eastern US are cultural parks that were set aside to preserve important historical events (e.g., Fort Necessity NB, Gettysburg NMP, Manassas NBP, Saratoga National NHP), and/or the homes of important historical figures (e.g., Home of Franklin D. Roosevelt NHS, George Washington Birthplace NM, and Booker T. Washington NM). While the land use histories prior to park establishment are not well known for all parks in this analysis, where known, they typically reflect the patterns of European settlement, land clearing, and agricultural abandonment of their region (e.g., National Park Service 2007, 2009a, 2009b, 2011). This study includes 39 national parks where forest monitoring is currently being implemented by the NPS I&M program, and where methods allow for direct comparisons of tree density with 7.31 m radius USFS-FIA subplots.

For this study, we used the most recent complete set of forest plot surveys for each park, which typically was 2013–2016, but ranged from 2011–2016. Because many diversity metrics are sensitive to differences in area and/or numbers of individuals (Crawley and Harral 2001), and to ensure that comparisons between NPS I&M and USFS-FIA forest plots were comparable, we only included live trees within 7.31 m radius of the center of each NPS forest plot to match the area of a USFS-FIA subplot. Additionally, we only included live trees ≥12.7 cm diameter at breast height (DBH) to match USFS-FIA's minimum tree DBH (USFS 2016). For more details on NPS I&M sample design and survey methods, refer to network and/or park-specific protocols (Comiskey et al. 2009b; Perles et al. 2014; Schmit et al. 2014; and Tierney et al. 2015).

2.2 Matrix Characterization

To characterize the matrix surrounding each park, we included USFS-FIA Phase 2 (i.e. ground-sampled) plots that had at least one fully forested and sampled 7.31 m radius subplot and that were located in the same ecological subsection as each park (US Forest Service 2015). Parks that crossed multiple ecological subsections included USFS-FIA plots from all of the ecological subsections crossed by the park to represent their matrix. Ecological Subsections are contiguous areas that have the same potential natural vegetation communities due to shared geology, topography and climate (ECOMAP 1993). Forests in parks and surrounding lands are largely second growth and share similar land-use histories prior to park establishment. Therefore, by comparing forest plots in parks with USFS-FIA plots in the same Ecological Subsection, observed differences should be primarily due to different management regimes, rather than environmental or climatic differences. We used the publicly available fuzzed, swapped USFS-FIA plot locations (http://www.fia.fs.fed.us/tools-data/, accessed April 2017), and included plot surveys from the most recent population evaluation group for each state that were available at the start of this study. The population evaluation groups ranged from 2014–2015 and included surveys from 2009–2015, depending on the length of survey cycle in each state, which ranged from 5 to 7 years. Although the year of observations of plots varied by as much as six years, there should be little difference in species composition across the time period, as we only examined adult trees which turn over slowly. We downloaded the relevant USFS-FIA data tables by state and performed all USFS-FIA data queries directly in R 3.4.0 (R Core Team 2017), and provide the code we used as supplementary material.

While USFS-FIA plots typically have four subplots, we only included the first (based on the subplot order) fully forested and sampled subplot per FIA plot so that subplots from the same plot were not sampled together in the same bootstrap iteration (see below). USFS-FIA subplots that fell within parks, based on ownership designations, were excluded from the analysis because we wanted to explicitly compare the tree diversity in park forests with non-park (i.e., matrix) forests.

To compare alpha diversity metrics between park and matrix forests, we generated a sampling distribution for each diversity metric using bootstrapping with replacement across 1000 replications of randomly selected USFS-FIA subplots within each park's corresponding matrix. To ensure comparisons were compatible between park and matrix forests, each of the 1000 bootstrap replications selected the same number of USFS-FIA subplots as the number of forest plots sampled by the NPS I&M program in the corresponding park. The only exception is Acadia National Park (ACAD), where the number of NPS I&M forest plots exceeded the number of USFS-FIA plots in the Ecological Subsection (171 forest plots in ACAD vs. 96 USFS-FIA subplots). In this case, we selected 50 NPS I&M forest plots in ACAD based on their Generalized Random-Tessellation Stratification (GRTS) priority to calculate the means for each diversity metric. GRTS is an algorithm that generates a spatially balanced randomized sample of locations (Stevens and Olsen 2004), and was used by the NPS I&M networks to determine forest plot locations. Selecting the first 50 consecutive forest plots in ACAD based on their GRTS priority therefore provided a spatially balanced, representative sample of forest plots in the park. We then used 50 as the number of USFS-FIA plots for each bootstrap sample to compare with ACAD. We used the bootstrapped USFS-FIA subplot (hereafter referred to as plot) data to generate a sampling distribution of each alpha diversity metric of interest for each park's surrounding matrix, and compared the matrix sampling distribution with the corresponding mean diversity metric from each park.

For comparisons of beta diversity between park and matrix forests, we used the same set of USFS-FIA plots from the alpha diversity analysis to represent each park's surrounding matrix. However, for the beta diversity analysis, we calculated beta diversity metrics (e.g., Jaccard similarity) and distances between all combinations of USFS-FIA plot pairs in each park's matrix, rather than bootstrapping a sampling distribution. Finally, to determine how the total number of species in each matrix varied and potentially explained diversity patterns, we calculated the regional species pool. The regional species pool was represented as the total number of tree species that were present across all of the USFS-FIA subplots corresponding to a park's matrix to examine how the regional species pool may affect diversity patterns observed across the study area (e.g. latitudinal gradients).

2.3 Diversity Metric Calculations

Following recommendations by McGill (2011), we calculated five alpha diversity metrics for each plot: number of individuals, tree species richness, Shannon Evenness, McNaughton Dominance, and Percent Rare N/S (# individuals/# species). We chose these five metrics because they quantify different aspects of the species abundance distribution and were found by McGill (2011) to be relatively independent of one another (except for richness and number of individuals) and high performing metrics even with small sample sizes. Number of individuals is the number of live tree stems ≥12.7 cm DBH that were present. Richness is simply the number of species present. Shannon Evenness is a measure of how similar relative abundances are among species, with higher values indicating greater diversity (Mauer and McGill 2011). We used the BiodiversityR package in R to calculate Shannon Evenness (i.e., Jevenness; Kindt and Coe 2005). McNaughton Dominance is the sum of the relative abundance of the two most abundant species, with lower values indicating greater diversity (McNaughton and Wolf 1970). Percent Rare N/S is the percent of species that have fewer individuals than the abundance of an average species on the plot (Maurer and McGill 2011). Higher percent Rare N/S values indicate higher diversity, although this metric is best interpreted in combination with the other diversity metrics. Shannon Evenness, McNaughton Dominance and Percent Rare N/S all range between 0 and 1. For a thorough description of each metric and their interpretation, see Box 5.1 in Maurer and McGill 2011. Peet (1974) also provides a helpful review of alpha diversity metrics. We calculated plot-level alpha diversity metrics including all live trees ≥12.7 cm DBH within the 7.31 m of plot center for all NPS I&M plots and with USFS-FIA plots in our sample. To remove the potential influence of different stem densities (i.e., number of individuals) between park and matrix forests, we also calculated alpha diversity metrics for the five live trees that were closest to the center of each NPS I&M plot and USFS-FIA plot in our sample. We selected five as the number of trees in this part of the analysis to maximize the number of USFS-FIA plots that were available for the analysis, while still having enough individuals to calculate diversity metrics.

To assess beta diversity of tree species, which is the turnover of species among sites, we calculated multiple metrics of similarity between all pairs of NPS I&M plots per park and all pairs of USFS-FIA plots per corresponding matrix using all live trees ≥12.7 cm DBH within the 7.31 m radius plot area. We calculated incidence-based metrics of beta diversity, which treat all species equally, and abundance-based metrics of beta diversity, which give higher weight to common species. For incidence-based metrics, we calculated Jaccard and Sørenson similarity indices, two commonly used incidence-based beta diversity metrics in plant ecology (Koleff et al. 2003; Barwell et al. 2015). We also calculated β_{SIM}, which was derived by Lennon et al. (2003) from Simpson's asymmetric index and found to be a robust incidence-based diversity metric that is less influenced by differences in richness between sites than Jaccard and Sørenson (Koleff et al. 2003; Barwell et al 2015). For abundance-based beta diversity metrics, we calculated $\beta_{MORISITA}$ and β_{HORN}, which have been shown to be high-performing abundance based diversity metrics, such as being insensitive to sample size and differences in species richness (Beck et al. 2013; Barwell et al. 2015). For each pair of plots that we calculated similarity metrics for, we also calculated the geographic distance between the plots using the pointDistance function in the raster package in R (Hijmans 2016).

2.4 Statistical Analysis

For the alpha diversity analysis, we calculated the mean for each diversity metric using the bootstrapped sampling distribution per matrix and compared it with the mean diversity metric in the corresponding park. Our bootstrapping approach avoids issues of unequal sample sizes and variance between park and matrix forests that other common approaches, such as t-tests would have. Uneven sample size is especially important to control for in biodiversity metrics, because many metrics like species richness are strongly correlated with sample size (Crawley and Harral 2001, McGill 2011). We calculated p-values for each metric by comparing the park mean to the empirical cumulative distribution function of the bootstrapped sampling distribution in the corresponding matrix, using a two-tailed test. We controlled for multiple comparisons by converting p-values to q-values with alpha=0.05 as the Type I error rate (Storey 2003; Dabney and Storey 2015) for all park/matrix comparisons per diversity metric. Because each park versus matrix comparison was based on the number of forest plots that were located in the corresponding park (i.e., varying number of plots between parks), and given the sensitivity of diversity metrics to differences in scale, mean diversity metrics were not comparable across parks. To account for this and to improve visual interpretation of the patterns across parks, we calculated the percent difference in mean diversity between each park and matrix pair. Percent difference is dimensionless and therefore more comparable across parks. Using this approach, a negative percent difference value indicates that the park metric was lower than the matrix, whereas a positive value indicates that the park metric was higher than the matrix. This approach assumes that the relationship between diversity metrics and number of plots is linear, which may not always be true. However, it should be roughly linear in a small region. Additionally, we only used the percent difference to improve visual interpretation of the results, not the statistical analysis, which our results and conclusions are based on.

We assessed beta diversity as a function of the decay in similarity between plots as geographic distance increases, where a steeper decay in similarity indicates higher beta diversity (Condit et al. 2002, Jurasinski et al. 2009), and therefore lower homogeneity in composition among sites. We examined distance decay in similarity at two scales: all combinations of plot pairs in each matrix (i.e., full matrix), and only matrix plot pairs that were within the range of the maximum distance between plot pairs within a park (i.e., subsetted matrix). Both scales included all combinations of plot pairs within a park. Because the maximum distance between plot pairs in a few parks was sometimes smaller than the minimum distances between matrix plot pairs, the following parks were removed from the smaller subsetted distance decay analysis: Johnstown Flood NM (JOFL), Saint-Gaudens NHS (SAGA), Thomas Stone NHS (THST), Weir Farm NHS (WEFA), and Wolf Trap Park for the Performing Arts (WOTR). For each park and matrix comparison, we used the diffslope function in the simba package in R (Jurasinski and Retzer 2012) to calculate the slope of the log-transformed similarity metric and distance for each park and matrix, and to test whether the slope was significantly different between each park and corresponding matrix. We log-transformed similarity and untransformed distance in the analysis based on findings in Nekola and White (1999) that this approach produced the most linear model. Using this model, a significantly steeper slope in one dataset indicates higher species turnover at shorter distances and thus higher beta diversity than a dataset with a shallower slope (Condit et al. 2002). Note that using the publicly available fuzzed USFS-FIA plot locations may add noise to this analysis, but because the fuzzed distances and directions are random, this should not affect the overall direction of the results (i.e., steeper or shallower slope). All statistical analyses were performed in R 3.4.0 (R Core Team 2017), and the R code used in this study is provided as supplementary material.

3. Results

3.1 Alpha Diversity

At the 7.31 m radius plot scale, parks tended to have fewer individuals (i.e., number of live stems) per plot than their corresponding matrix (69% of parks; Figure 2). At this same scale, species richness tended to be higher than matrix forests for 61% of the parks. However, given the sensitivity of species richness to number of individuals, the tendency for more trees per plot in matrix forests may be obscuring the tendency for parks to have greater richness. Patterns of Shannon evenness were more distinct, with

74% of parks having greater evenness of tree species than matrix forests. Despite tending to have fewer individuals per plot, park forests also had lower McNaughton Dominance (69% of parks) and higher percent of rare species, based on % Rare N/S (61% of parks). There were also slight latitudinal gradients in the diversity patterns, with parks at lower latitudes more consistently having higher richness, lower McNaughton dominance, and higher percent rare species than parks at higher latitudes. Regional species pools were smaller for the more northern parks in this study (Table 2), which may partially explain the latitudinal gradients observed in the percent rare metrics. In other words, northern parks had fewer species in the regional species pool to contribute to diversity metrics.

Patterns of species richness between park and matrix forests were more distinct after controlling for number of individuals by consistently including only the five closest trees to the center per plot. At this scale, higher species richness was observed in 77% of parks compared to matrix forests (Figure 3). Despite including only five trees, park forests still tended to be more even in abundance (61% of parks) and had a higher percent of rare species (61% of parks) than matrix forests. Park forests were also less dominated than matrix forests, with 74% of parks having lower mean McNaughton Dominance than matrix forests. At the scale of five individuals, the latitudinal gradient for species richness was not present and the McNaughton Dominance latitudinal gradient was much weaker.

Taken together, alpha diversity results suggest that, particularly after removing the influence of the number of individuals, parks tend to have greater alpha diversity than matrix forests, with higher species richness and a more even, less dominated distribution of abundance across species. This pattern was observed in the majority of parks in the analysis, but was most consistent in lower latitude parks. Several parks did have lower site-level alpha diversity than their surrounding matrix forests, and they were typically the most northern parks, including ACAD, Friendship Hill NHS (FRHI), Johnstown Flood NM (JOFL), Marsh-Billings-Rockefeller NHP (MABI), Minute-Man NHP (MIMA), Saratoga NHP (SARA) and Weir Farm NHS (WEFA).

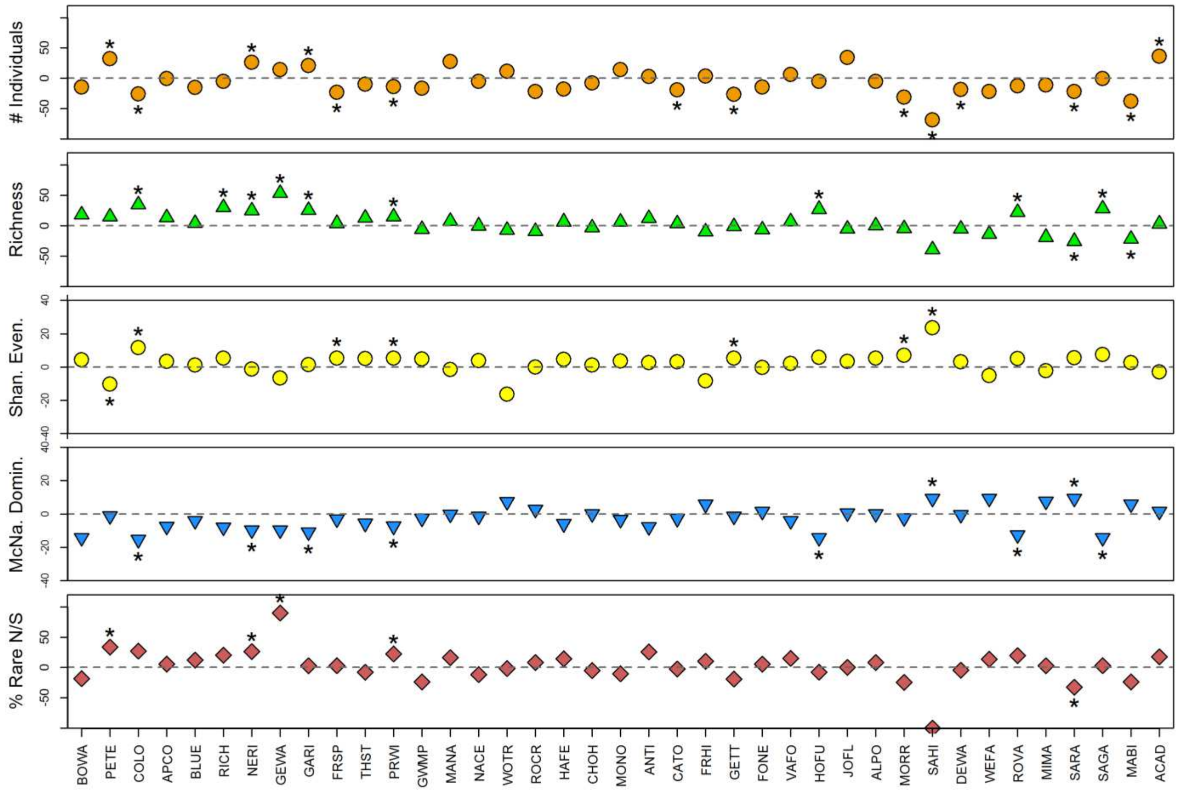

Figure 2. Percent difference between park and matrix diversity metrics for all live trees within 7.31 m radius. Metrics include number of individuals, species richness, Shannon Evenness (Shan. Even.), McNaughton Dominance (McNa. Domin.), and Percent Rare N/S (% Rare N/S). Positive values indicate higher mean values for parks than matrix. Negative values indicate lower mean values for parks than matrix. Note that negative percent differences for McNaughton Dominance indicate higher diversity in parks. Stars indicate that the difference is significant. Parks are ordered from low to high latitude. Metric symbols and colors are consistent with Figure 3.

Network	Park	# USFS-FIA subplots	Regional Species Pool
ERMN	ALPO	237	47
	BLUE	61	36
	DEWA	205	46
	FONE	119	30
	FRHI	833	73
	GARI	417	61
	JOFL	298	47
	NERI	621	66
MIDN	APCO	274	44
	BOWA	274	44
	FRSP	2015	87
	GETT	109	51
	HOFU	109	51
	PETE	1656	86
	RICH	769	72
	VAFO	214	61
NCBN	COLO	1015	75
	GEWA	246	43
	SAHI	36	21
	THST	86	40
NCRN	ANTI	257	58
	CATO	177	48
	CHOH	1321	89
	GWMP	241	56
	HAFE	383	61
	MANA	50	34
	MONO	50	34
	NACE	86	40
	PRWI	937	71
	ROCR	191	53
	WOTR	50	34
NETN	ACAD	96	22
	MABI	119	30
	MIMA	205	38
	MORR	142	57
	ROVA	96	39
	SAGA	119	30
	SARA	43	36
	WEFA	248	47

Table 2. Information on matrix forests surrounding parks in this study.

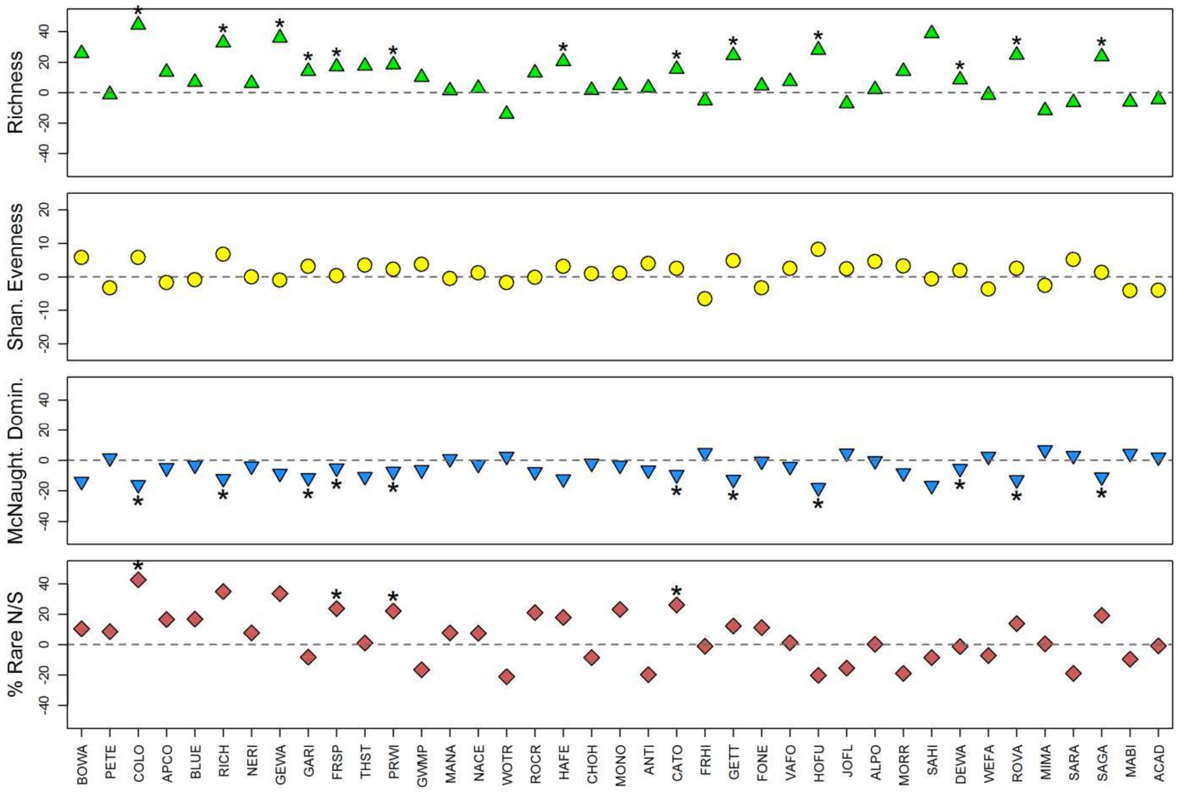

Figure 3. Percent difference between park and matrix diversity metrics for the 5 closest trees. Metrics include species richness, Shannon Evenness (Shan. Even.), McNaughton Dominance (McNa. Domin.), and Percent Rare N/S (% Rare N/S). Positive values indicate higher mean values for parks than matrix. Negative values indicate lower mean values for parks than matrix. Stars indicate that the difference is significant. Parks are ordered from low to high latitude.

3.2 Beta Diversity

At the full matrix scale, parks usually had steeper slopes of similarity decay with distance than matrix forests across all five similarity metrics (Figure 4). The beta diversity metrics in our study treat shared and unshared species components differently in their calculations. These metrics also weigh species differently based on their abundance, with Sørensen, Jaccard, and β_{SIM} treating all species equally, and $\beta_{MORISITA}$ and β_{HORN} giving more weight to abundance species. The consistent pattern across all of the metrics in our study therefore provides strong evidence that beta diversity differs between park and matrix forests. These results suggest that park forests had higher beta diversity and were less homogenous than matrix forests. Notable exceptions to this pattern were parks in the Eastern Rivers and Mountains Network (ERMN), including Bluestone NSR (BLUE), New River Gorge NR (NERI), FRHI, Allegheny Portage Railroad NHS (ALPO), and Delaware Water Gap NRA (DEWA), which all had a significantly shallower slope than their corresponding matrix. These results indicate that the forests in these ERMN parks were potentially more homogenous than their corresponding matrix forests.

Given that parks in our analysis were considerably smaller in area than their surrounding matrix, the patterns of distance decay in similarity could be strongly influenced by the differences in scale between park and matrix datasets. After subsetting the matrix datasets to only include matrix plot pairs that were within the maximum distance between plot pairs in their corresponding park, patterns were less distinct (Figure 5). Differences in slopes between park and matrix forests tended to be smaller and fewer parks had significantly different slopes than matrix forests. These results suggest that at the scale of parks, distance decay in tree species similarity does not differ significantly from matrix forests. However, it is unclear if this is due to an actual similarity in beta diversity between parks and matrix or a loss of power to detect a difference due to a smaller sample and a shorter range of distances over which a decay of similarity curve is fit.

4. Discussion

Parks in our study consistently had higher tree species richness (particularly after controlling for the influence of the number of individuals), higher Shannon Evenness, lower McNaughton Dominance, and a higher percentage of rare species than surrounding matrix forests. Patterns were most consistent for the southern parks in this study. At the full matrix scale, parks also consistently had a steeper distance decay in similarity. These results suggest that protected areas, such as the national parks in our study, tend to have greater alpha diversity of tree species and are potentially less homogenous across sites than unprotected forests. Management practices in parks, such as removing invasive species and restoring

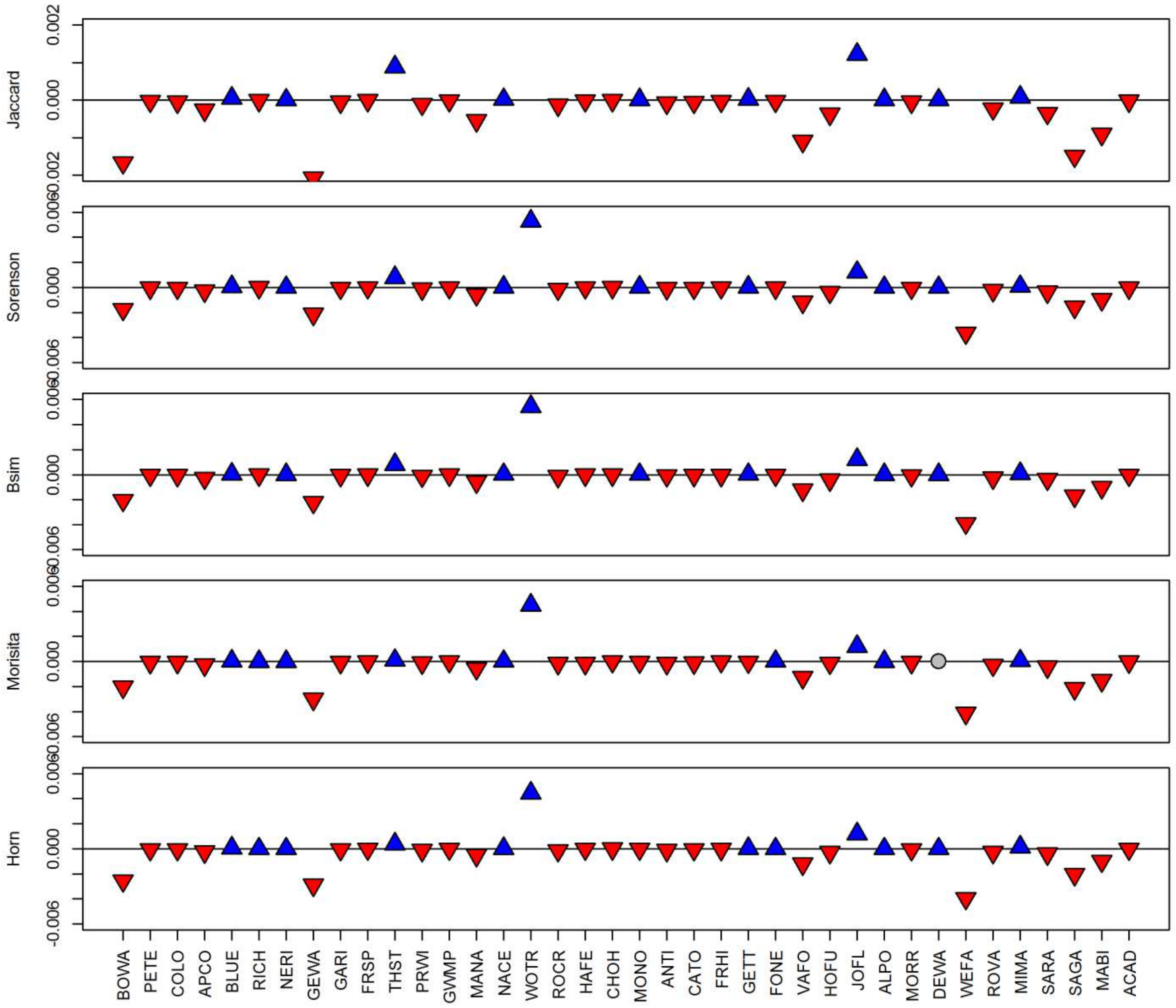

Figure 4. Differences in slope of distance decay in similarity between each park and full matrix. Red, downward pointing triangles indicate that a park slope is significantly steeper than the matrix slope. Blue, upward pointing triangles indicate that a matrix slope is significantly steeper than the park slope. Grey circles are not significant. Parks are ordered from low to high latitude.

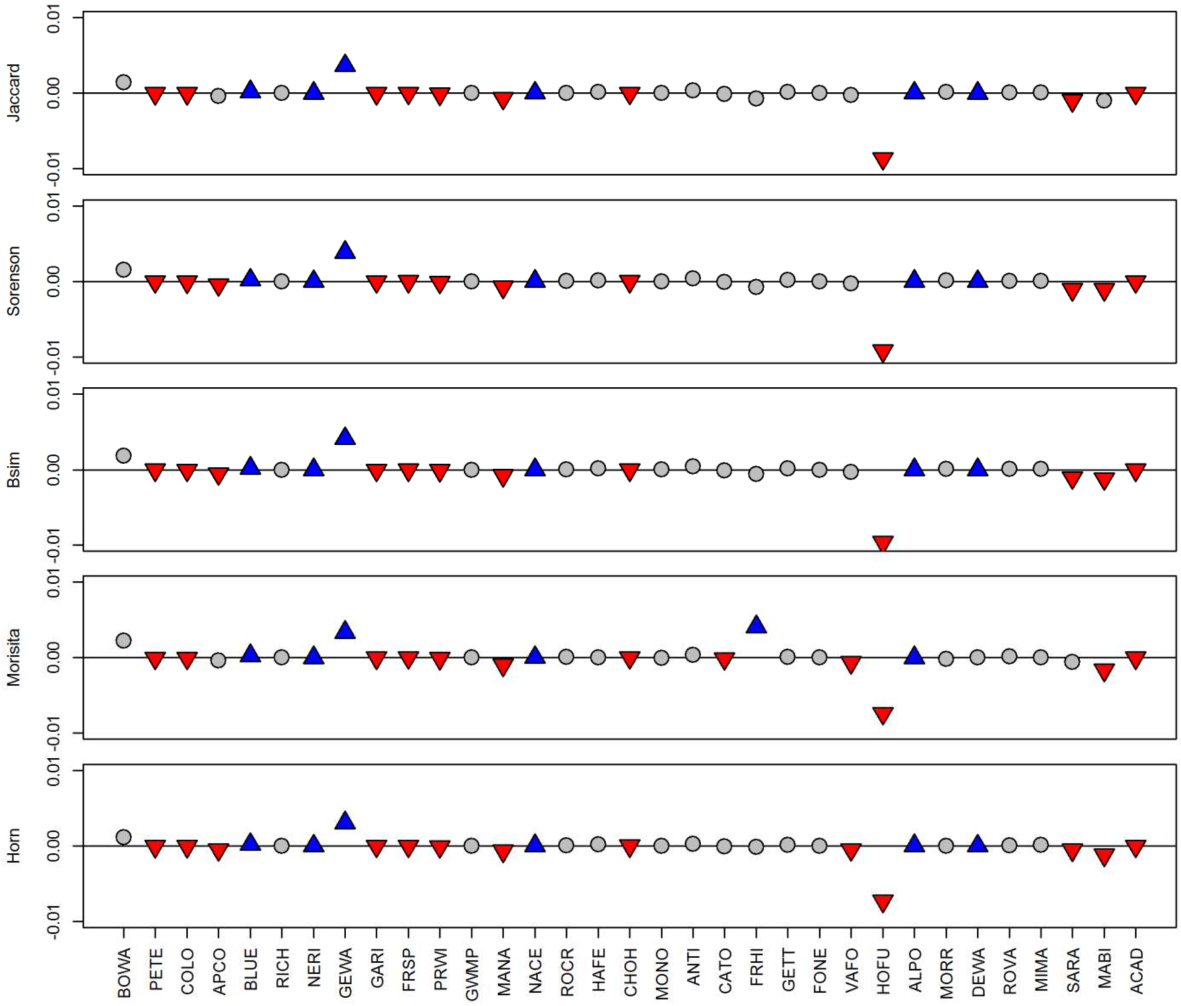

Figure 5. Differences in slope of distance decay in similarity between each park and matrix that only includes distances between plots represented within parks. Red, downward pointing triangles indicate that a park slope is significantly steeper than the matrix slope. Blue, upward pointing triangles indicate that a matrix slope is significantly steeper than the park slope. Grey circles are not significant. Parks are ordered from low to high latitude.

degraded habitats, likely explain some of these diversity patterns, as the matrix forests surrounding parks are largely under private ownership (Miller et al. 2016) and less likely to receive that level of management. In addition, many of the parks in our study have been allowed to develop under natural disturbance regimes and have been protected from timber harvesting for many decades to over a century. Given that 73% of the forestland in the southern part of our analysis and 40% of the forestland in the northern part of our analysis are composed of stands that are less than 60 years old (Oswalt et al. 2014), protection from harvesting is likely an important factor in the differences we observed between park and matrix forests. However, because we do not have the management histories of the matrix forests, we are unable to determine the level of influence timber harvesting and the various harvesting methods have on the patterns we observed. Similar impacts of forest management on tree diversity have been documented, although they typically have focused on species richness (e.g., Clark and Covey 2012), were restricted to a specific forest biome (e.g., Boucher et al. 2015), or were only conducted at stand-level scales (e.g., Shuler 2004; Neuendorff et al. 2007; Keyser and Loftis 2012). Our study is the first to document consistent differences in tree diversity between protected and unprotected forests across multiple metrics and scales and while covering multiple forest biomes (e.g., boreal, northern hemlock-hardwood, and oak-hickory forests).

While most parks followed the pattern of greater alpha diversity than matrix forests, there were several parks that consistently had lower alpha diversity than matrix forests, including ACAD, FRHI, JOFL, MABI, MIMA, SARA, and WEFA. These tended to be the more northern parks in the study, which had also smaller regional species pools than southern parks. Future studies to examine the underlying causes of lower site-level diversity in these parks, particularly whether they are driven by natural process (e.g., succession) or are the result of human-caused stressors (e.g., deer overabundance, fire suppression, etc.), will be important information for park managers. These parks may be more vulnerable to climate change and other stressors than matrix forests, and could benefit from management strategies that seek to increase species diversity, such as assisted migration of species that may be more adapted to climate changes in that park (Millar et al. 2007). Continued monitoring and adaptive management will be important to ensure these parks maintain forest diversity and function over time.

The results from our study demonstrate the value of examining multiple metrics to explore patterns of tree diversity including number of individuals, species richness and metrics that characterize the shape of the species abundance distribution. For example, at the 7.31 m radius plot area, tree species richness patterns were somewhat obscured by the fact that parks tended to have fewer trees per plot. However, there were clear differences in other diversity metrics, with park forests being less dominated by a few species and having a more even abundance distribution across species. Our study also demonstrates the influence that number of individuals can have on species richness. We attempted to control for this by using equal plot areas and equal number of plots in comparisons between parks and matrix forests, but numbers of individuals between parks and matrix forests at the 7.31 m radius plot area still varied. After selecting only five individuals per plot, the species richness pattern became clearer, with parks having consistently higher richness than matrix forests. Despite only including five individuals, patterns of the remaining diversity metrics were consistent with the full plot analysis.

Results from the beta diversity analysis at the full matrix scale tentatively suggested that parks were less homogenous across sites than matrix forests. However, it is important to note that our beta diversity results were exploratory, as differences in scale in the full matrix analysis and small sample sizes at compatible scales in the subsetted matrix analysis impaired our ability to fully examine patterns of beta diversity between park and matrix forests. Using the real USFS-FIA plot locations rather than the fuzzed locations may reveal stronger patterns as well. The patterns of beta diversity for parks in Eastern Rivers and Mountains Network (ERMN) also warrant further investigation. In contrast to the other regional networks in this analysis, ERMN had multiple parks with a shallower slope than their corresponding matrix, suggesting that the forests in these parks are more homogenous than matrix forests. Another possibility is that environmental gradients in the matrix were not represented in parks. While this is beyond the scope of our study, incorporating gradients as covariates, such as elevation or soil type, may help determine whether missing environmental gradients explain the homogeneity in ERMN park forests.

Despite the drawbacks of our beta diversity analysis, this is the first study we are aware of that examines how forest protection influences beta diversity. Our results show promise for future research on beta diversity in eastern forests, particularly for studies conducted at compatible scales and that can incorporate environmental gradients as covariates.

A number of studies examining the impacts of forest management on tree diversity have documented a decoupling of forest composition with local environmental and climatic gradients (White 2012; Thompson et al. 2013; Boucher et al. 2015). For example, Thompson et al. (2013) found the association between temperature and northeastern tree species composition to weaken dramatically between pre-colonial times and current day. While Thompson et al. (2013) investigated the influence of land use on the patterns they observed, they did not examine whether protected areas responded differently over time. Future studies investigating whether tree species composition in protected areas have stronger relationships with environmental and climatic gradients compared with unprotected forests could improve predictions for how forests under different management regimes will respond to climate change and other stressors.

Combining the results of this study with those of Miller et al. (2016), which found parks to have consistently greater structural complexity than matrix forests, park forests may respond differently to climate change and other stressors than managed forests. Given their greater species diversity and structural complexity, park forests may also have greater response variability to climate change, as there is a higher chance that at least some of the tree species or size cohorts present will persist through climate change (Evans and Perschel 2009; Brockerhoff et al. 2017; D'Amato et al. 2011). However, it is important to note that greater diversity does not always lead to greater resilience, particularly if functionally equivalent species are likely to respond similarly to change (e.g., sensitive to drought). In addition, forests with naturally low species diversity, such as jack pine (*Pinus banksiana*) forests, may be more resilient than other forests to disturbance because they are well-adapted for stand-replacing fire disturbances (Chapin et al. 2004). We also have yet to compare functional diversity of trees in protected and matrix forests, which is another important factor likely to influence forest resilience and adaptive capacity

(Elmquist et al. 2003). Although many parks contain greater tree diversity, invasive species, forest pests, and elevated deer populations are an ongoing threat to forest diversity. Management practices that reduce these stressors are important to ensure that parks maintain structurally and compositionally diverse forests long term. Continued monitoring in protected and matrix forests is also important to determine how forests respond to climate change and whether specific management actions, such as protecting more forests, translocating species, or altering management practices, are necessary to maintain biodiversity and function of eastern forests.

Acknowledgments

Funding for this research was provided by the National Park Service Inventory and Monitoring Program. We would like to thank the U.S. Forest Service Forest Inventory and Analysis Program for making their data publicly available. We are also grateful to all of the field crews who collected the data for this study.

References

Amatangelo, K. L., M. R. Fulton, D. A. Rogers, D. M. Waller. 2011. Converging forest community composition along an edaphic gradient threatens landscape-level diversity. Diversity and Distributions 17:201-213.

Aussenac, R., Y. Bergeron, C. G. Mekontchou, D. Gravel, K. Pilch, and I. Drobyshev. 2017. Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing affect of species diversity on forest growth. Journal of Ecology 105:1010-1020.

Barbier, S., F. Gosselin, and P. Balandier. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – A critical review for temperate and boreal forests. Forest Ecology and Management 254: 1-15.

Barwell, L. J., N. J. B. Isaac, and W. E. Kunin. 2015. Measuring β-diversity with species abundance data. Journal of Animal Ecology 84:1112-1122.

Beck, J., J. D. Holloway, and W. Schwanghart. 2013. Undersampling and the measurement of beta diversity. Methods in Ecology and Evolution 4: 370-382.

Belote, R. T., S. Prisley, R. H. Jones, M. Fitzpatrick, and K. de Beurs. 2011. Forest productivity and tree diversity relationships depend on ecological context within mid-Atlantic and Appalachian forests (USA). Forest Ecology and Management 261:1315-1324.

Bolton, N. W., and A. W. D'Amato. 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. Forest Ecology and Management 262: 1215-1222.

Boucher, D., L. D. Grandpré, D. Kneeshaw, B. St-Onge, J. C. Ruel, K. Waldron, and J. M. Lussier. 2015. Effects of 80 years of forest management on landscape structure and pattern in the eastern Canadian boreal forest. Landscape Ecology 30:1913-1929.

Boucher, Y., D. Arseneault, L. Sirois, L. Blais. 2009. Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. Landscape Ecology 24:171-184.

Brockerhoff, E. G., L. Barbaro, B. Castagneyrol, D. I. Forrester, B. Gardiner, J. R. González-Olabarria, P. O. Lyver, N. Meurisse, A. Oxbrough, H. Taki, I. D. Thompson, F. van der Plas, and H. Jactel. 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodiversity and Conservation 26:3005-3035.

Brose, P. H., D. C. Dey, R. J. Phillips, and T. A. Waldrop. 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in Eastern North America? Forest Science 59(3):322-334.

Canham, C. D., and R. Q. Thomas. 2010. Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. Ecology 91(12):3433-3440.

Chapin, F. S. III., T. V. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. Zimov. 2004. Global change and the boreal forest: Thresholds, shifting states or gradual change? Ambio 33: 361-365.

Clark, J. A., and K. R. Covey. 2012. Tree species richness and the logging of natural forests: a meta-analysis. Forest Ecology and Management 276:146-153.

Coetzee, B. W. T., K. J. Gaston, and S. L. Chown. 2014. Local scale comparisons of biodiversity as a test for global protected area ecological performance: a meta-analysis. PLoS ONE 9(8): e105824. doi:10.1371/journal.pone.0105824

Comiskey, J. A., J. P. Schmit, S. Sanders, J. P. Campbell, and B. R. Mitchell. 2009a. Forest vegetation monitoring in eastern parks. Park Science 26:76–80.

Comiskey, J. A., J. P. Schmit, and G. L. Tierney. 2009b. Mid-Atlantic Network forest vegetation monitoring protocol. Natural Resource Report NPS/MIDN/NRR—2009/119 National Park Service, Fort Collins, Colorado.

Condit, R, N. Pitman, E. G. Leigh, Jr., J. Chave, J. Terborgh, R. B. Foster, P. V. Nunez, S. Aguilar, R. Valencia, G. Villa, J. C. Muller-Landau, E. Losos, and S. Hubbell. 2002. Beta-diversity in tropical forest trees. Science 295:666-669.

Côte, S. D., T. P. Rooney, J-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review Ecology, Evolution, and Systematics 35:113-147.

Côte, S. D., J. Beguin, S. de Bellefeuille, E. Champagne, N. Thiffault, and J-P. Tremblay. 2014. Structuring effects of deer in boreal forest ecosystems. Advances in Ecology DOI: 10.1155/2014/917834.

Crawley, M. J., and J. E. Harral. 2001. Scale dependence in plant biodiversity. Science 291(5505):864-868.

Dabney, A., and J. D. Storey. 2015. qvalue: Q-value estimation for false discovery rate control. R package version 2.2.0. http://qvalue.princeton.edu//

D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2011. Forest management for mitigation and adaptation to climate change: insights from long-term silvicultural experiments. Forest Ecology and Management 262:803-816.

ECOMAP. 1993. National hierarchical framework of ecological units. US Department of Agriculture, Forest Service, Washington D.C., USA.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliot, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3(9):479-486.

Elmquist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment. 1: 488-494.

Evans, A. M., and R. Perschel. 2009. A review of forestry mitigation and adaptation strategies in the Northeast US. Climate Change 96:167-183.

Flower, C. E., K. S. Knight, M. A. Gonzalez-Meler. 2013. Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biological Invasions 15:931-944.

Gamfeldt, L., T. Snäll, R. Bagchi, M. Jonsson, L. Gustafsson, P. Kjellander, M. C. Ruiz-Jaen, M. Fröberg, J. Stendahl, C. D. Philipson, G. Mikusiński, E. Andersson, B. Westerlund, H. Andrén, F. Moberg, J. Moen, and J. Bengtsson. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4:1340. DOI:10.1038/ncomms2328

Gray, C. L., S. L. L. Hill, T. Newbold, L. N. Hudson, L. Börger, S. Contu, A. J. Hoskins, S. Ferrier, A. Purvis, and J. P. W. Scharlemann. 2015. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nature Communications 7:12306. DOI: 10.1038/ncomms12306

Hanberry, B., B. J. Palik, and H. S. He. 2012. Comparison of historical and current forest surveys for detection of homogenization and Mesophication of Minnesota forests. Landscape Ecology 27:1495-1512.

Hijmans, R. J. 2016. raster: Geographic data analysis and modeling. R package version 2.5-8. http://CRAN.R-project.org/package=raster.

Hobson, K. A., and E. Bayne. 2000. Breeding bird communities in boreal forest of western Canada: consequences of "unmixing" the mixed woods. The Condor 102:759-769

Jactel, H. and E. G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. Ecology Letters 10:835-848.

Janowiak, M. K., C. W. Swanston, L. M. Nagel, L. A. Brandt, P. R. Butler, S. D. Handler, P. D. Shannon, L. R. Iverson, S. N. Matthews, A. Prasad, and M. P. Peters. 2014. A practical approach for translating climate change adaptation principles into forest management actions. Journal of Forestry 112(5):242-433.

Jurasinski, G., V. Retzer, and C. Beierkuhnlein. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. Oecologia 159(1): 15-26.

Jurasinski, G., and V. Retzer. 2012. simba: A collection of functions for similarity analysis of vegetation data. R package version 0.3-5. https://CRAN.R-project.org/package=simba.

Kern, C. C., J. I. Burton, P. Raymond, A. W. D'Amato, W. S. Keeton, A. A. Royo, M. B. Walters, C. R. Webster, and J. L. Willis. 2017. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. Forestry 90: 4-17.

Keyser, T. L., and D. L. Loftis. 2012. Long-term effects of single-tree selection cutting on structure and composition in upland mixed-hardwood forests of the southern Appalachian Mountains. Forestry 86:255-265.

Kindt, R., and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecology and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi. ISBN 92-9059-179-X.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72:367-382.

Lefcheck, J. S., J. E. K. Byrnes, F. Isbell, L. Gamfeldt, J. N. Griffin, N. Eisenhauer, M. J. S. Hensel, A. Hector, B. J. Cardinale, and J. E. Duffy. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature Communications 6:6936.

Loo, J. A. 2009. Ecological impacts of non-indigenous invasive fungi as forest pathogens. Biological Invasions 11:81-96.

Lorimer, C. G., and A. S. White. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management 185: 41-64.

Matonis, M. S., M. B. Walters, J. D. A. Millington. 2011. Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. Forest Ecology and Management 262:286-298.

Maurer, B. A., and B. J. McGill. 2011. Measurement of species diversity. *In* A. E. Magurran & B. J. McGill (Eds.), Biological Diversity: frontiers in measurement and assessment (pp. 55- 65). Oxford University Press, Oxford.

McEwan, R. W., J. M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34:244-256.

McGill, B. J. 2011. Species abundance distributions. *In* A. E. Magurran & B. J. McGill (Eds.), Biological Diversity: frontiers in measurement and assessment (pp.105-122). Oxford University Press, Oxford.

McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. Science 167: 131-139.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17(8):2145-2151.

Miller, K. M., F. W. Dieffenbach, J. P. Campbell, W. B. Cass, J. A. Comiskey, E. R. Matthews, B. J. McGill, B. R. Mitchell, S. J. Perles, S. Sanders, J. P. Schmit, S. Smith, and A. S. Weed. 2016.

National parks in the eastern United States harbor important older forest structure compared with matrix forests. Ecosphere 7(7): e01404.10.1002/ecs2.1404

National Park Service. 2007. Battle Road: Cultural Landscapes Inventory, Minute Man National Historical Park, National Park Service. https://irma.nps.gov/DataStore/Reference/Profile/2185681.

National Park Service. 2009a. Sieur de Monts Springs: Cultural Landscape Inventory, Acadia National Park, National Park Service. https://irma.nps.gov/DataStore/Reference/Profile/2229080.

National Park Service. 2009b. Fort Necessity's CCC Picnic Area: Fort Necessity National Battlefield, National Park Service. https://irma.nps.gov/DataStore/Reference/Profile/2186011.

National Park Service. 2011. Ellwood: Cultural Landscape Inventory, Fredericksburg and Spotsylvania National Military Park, National Park Service. https://irma.nps.gov/DataStore/Reference/Profile/2194794.

Nekola, J.C., and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography 26:867-878.

Neuendorff, J. K., L. M. Nagel, C. R. Webster, and M. K. Janowiak. 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. Northern Journal of Applied Forestry 24(3):197-202.

Niese, J. N., and T. F. Strong. 1992. Economic and tree diversity trade-offs in managed northern hardwoods. Canadian Journal of Forest Management 22:1807-1813.

Nowacki, M. D., and G. J. Abrams. 2008. The demise of fire and “mesophication” of forests in the Eastern United States. BioScience 58(2): 123-138.

Nowacki, M. D., and G. J. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology 21:314-334.

Nuttle, T., A. A. Royo, M. B. Adams, and W. P. Carson. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecological Monographs 83(1):3-17.

Oswalt, S. N., W. B. Smith, P. D. Miles, and S. A Pugh. 2014. Forest resources of the United States, 2012. General Technical Report WO-91. US Department of Agriculture, Forest Service, Washington D.C., USA.

Paquette, A., and C. Messier. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Global Ecology and Biogeography 20:170-180.

Peet, R. K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5:285-307.

Perles, S. J., D. Finley, D. Manning, and M. Marshall. 2014. Vegetation and soil monitoring protocol for the Eastern Rivers and Mountains Network, Version 3. Natural Resource Report. NPS/ERMN/NRR—2014/758. National Park Service. Fort Collins, Colorado.

Rooney. T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165-176.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Salk, T.T., L. E. Frelich, S. Sugita, R. Calcote, J. B. Ferrari, and R. A. Montgomery. 2011. Poor recruitment is changing the structure and species composition of and old growth hemlock-hardwood forest. Forest Ecology Management 261:1998–2006.

Schmit, J. P., G. M. Mueller, P. R. Leacock, J. L. Mata, Q. Wu, and Y. Huang. 2005. Assessment of tree species richness as a surrogate for macrofungal species richness. Biological Conservation 121: 99-110.

Schmit, J. P., G. Sanders, M. Lehman, T. Paradis, and E. R. Matthews. 2014. National Capital Region Network Long-Term Forest Vegetation Monitoring Protocol: Version 2.1 (March, 2014). Natural Resource Report. NPS/NCRN/NRR—2009/113. National Park Service. Fort Collins, Colorado.

Schuler, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. Canadian Journal of Forest Research 34: 985-997.

Schulte, L. A., D. J. Mladenoff, T. R. Crow, L. C. Merrick, and D. T. Cleland. 2007. Homogenization of northern U.S. Great Lakes forests due to land use. Landscape Ecology 22:1089-1103.

Shields, J. M., C. R. Webster, and L. M. Nagel. 2007. Factors influencing tree species diversity and *Betula alleghaniensis* establishment in silvicultural openings. Forestry 80(3):293-307.

Siefert, A., C. Ravenscroft, M. D. Weiser, and N. G. Swenson. 2013. Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. Global Ecology and Biogeography 22:682-691.

Sobek, S., M. M. Gossner, C. Cherber, I. Steffan-Dewenter, and T. Tscharntke. 2009. Tree diversity drives abundance and spatiotemporal β-diversity of true bugs (Heteroptera). Ecological Entomology 34:772-782.

Storey, J. 2003. The positive false discovery rate: A Bayesian interpretation and the q-value. Annals of Statistics 31:2013-2035.

Thompson, J. R., D. R. Carpenter, C. V. Cogbill, and D. R. Foster. 2013. Four centuries of change in Northeastern United States forests. PLoS ONE 8(9):e72540. DOI:10.1371/journal.pone.0072540.

Tierney, G. L., B. R. Mitchell, K. M. Miller, J. A. Comiskey, A. J. Kozlowski, and D. Faber-Langendoen. 2015. Northeast Temperate Network long-term forest monitoring protocol: 2015 revision. Natural Resource Report NPS/NETN/NRR–2015/923. National Park Service, Fort Collins, Colorado.

US Forest Service. 2015. Ecological Subregions: Sections and subsections for the conterminous United States. U.S. Forest Service ECOMAP Team, Washington, D.C. http://apps.fs.fed.us/ArcX/rest/services/EDW/EDW_EcomapSections_01/MapServer

US Forest Service. 2016. Forest inventory and analysis national core field guide, Volume 1: Field data collection procedures for Phase 2 Plots, version 7.1. U.S. Department of Agriculture, Forest Service, Washington Office.

van der Plas, F., P. Manning, S. Soliveres, E. Allan, M. Scherer-Lorenzen, K. Verheyen, C. Wirth, M. A. Zavala, E. Ampoorter, L. Baeten, L. Barbaro, J. Bauhus, R. Benavides, A. Benneter, D. Bonal, O. Bouriaud, H. Bruelheide, F. Bussotti, M. Carnol, B. Castagneyrol, Y. Charbonnier, D. A. Coomes, A. Coppi, C. C. Bastias, S. M. Dawud, H. D. Wandeler, T. Domisch, L. Finér, A. Gessler, A. Granier, C. Grossiord, V. Guyot, S. Hättenschwiler, H. Jactel, B. Jaroszewicz, F. X. Joly, T. Jucker, J. Koricheva, H. Milligan, S. Mueller, B. Muys, D. Nguyen, M. Pollastrini, S. Ratcliffe, K. Raulund-Rasmussen, F. Selvi, J. Stenlid, F. Valladares, L. Vesterdal, D. Zielínski, and M. Fischer. 2016. Biotic homogenization can decrease landscape-scale forest multifunctionality. Proceedings of the National Academy of Sciences 113: 3557-3562.

Vilá, M., A. Carrilo-Gavilán, J. Vayreda, H. Bugmann, J. Fridman, W. Grodzki, J. Haase, G. Kunstler, M. Schelhaas, and A. Trasobares. 2013. Disentangling biodiversity and climatic determinants of wood production. PloS one 8(2): e53530.

Vose, J. E., D. N. Wear, A. E. Mayfield III, and C. D. Nelson. 2013. Hemlock woolly adelgid in the southern Appalachians: control strategies, ecological impacts, and potential management responses. Forest Ecology and Management 291:209-219.

White, M. A. 2012. Long-term effects of deer browsing: composition, structure and productivity in a northeastern Minnesota old-growth forest. Forest Ecology and Management 269:222-228.

Woodall, C. W., A. W. D'Amato, J. B. Bradford, and A. O. Finley. 2011. Effects of stand and inter-specific stocking on maximizing standing tree carbon stocks in the Eastern United States. Forest Science 57(5):365-378.