

Regional changes to forest understories since the mid-Twentieth Century: Effects of overabundant deer and other factors in northern New Jersey

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ABSTRACT

Increased densities of white-tailed deer (*Odocoileus virginianus*) in eastern North America cause multiple impacts to forest understories, but few studies have documented their effects at large spatial and temporal scales. I studied long-term, regional changes in forest understories in northern New Jersey, comparing data from 62 stands in 2014–2018 to historical data gathered from the same stands in 1948–1973, when statewide deer densities were substantially lower. Significant declines occurred in nearly all forest layers, including densities of large seedlings (80%), saplings (75%) and trees (18%), with parallel declines in the cover of native herbs (76%) and shrubs (72%). In contrast, the cover of exotic shrubs, lianas, and herbs increased by $5 \times$ – $40 \times$, resulting in a major shift in species composition away from mostly native species cover ($\geq 95\%$) to mostly exotic shrub and liana cover (54%). Significant changes in tree species composition were also observed in relation to deer browse preferences, especially in the large seedling and sapling layers, which exhibited the greatest declines. Sites with higher estimated deer populations show conspicuously lower sapling densities ($R^2 = 0.47$). Experimental data from nine deer exclosures of different ages showed consistent increases in large seedling density and heights over time, and full recovery of large seedling abundance and species composition to historic levels after 11–20 yrs. Native lianas and herbs and exotic shrubs each increased or maintained their dominance in exclosures. Species afflicted by introduced pests and diseases (e.g., *Cornus florida* and *Tsuga canadensis*) also declined greatly, but their declines were not sufficient to explain overall forest understory declines. Declines in tree recruitment could not be explained by changes in disturbance regimes and/or light levels over time. Because deer strongly reduce tree recruitment, shift species composition, and reduce understory cover across large spatial scales, they represent a significant concern for forest managers and an issue that should be effectively addressed.

1. Introduction

In the absence of natural predators, elevated populations of white-tailed deer (*Odocoileus virginianus*) have been reported throughout large portions of their range in recent decades (McWilliams et al., 2018), in many areas rising to levels that are historically unprecedented (McCabe and McCabe, 1997). The resulting increase in deer browse may impact any and all categories of forest understory vegetation, including trees, woody shrubs and lianas, herbaceous plants and seed banks (diTommaso et al., 2014; Russell et al., 2017; Russell et al., 2001; Rooney, 2009; Ashton and Lerdau, 2008; Côté et al., 2004; Waller and Alverson, 1997). The selective browsing by deer of certain plant species over others also leads to shifts in native species composition, loss of diversity, and increased prevalence of non-native plant species (Averill et al., 2018; Heckel et al., 2010; Eschtruth and Battles, 2009; Knight et al., 2009; Rooney, 2009; Horsley et al., 2003). These impacts to vegetation, in turn, translate into indirect effects on a myriad of other, associated forest species, including shrub and ground nesting birds (Baiser et al., 2008; McShea and Rappole, 2000), forest arthropods and insectivorous birds (Roberson et al., 2016; Nuttle et al., 2011), and small mammals (Byman, 2011; Brooks and Healy, 1988). Soils, nutrient flows, and other aspects of ecosystem function may also be affected (Sabo et al., 2017; Shelton et al., 2014; Didier, 2003). The increases in

non-native vegetation can likewise contribute to cascade effects in forest structure, fauna, food webs, soils, microclimates and assorted ecosystem functions (Bucciarelli et al., 2014; Burghardt et al., 2010; Ashton and Lerdau, 2008; Ehrenfeld et al., 2001).

Despite the wealth of research on this subject, studies of the effects of white-tailed deer on forest understories across large spatial and temporal scales are limited (Russell et al., 2017; Bradshaw and Waller, 2016; McGarvey et al., 2013; Russell et al., 2001). Given the variation in local deer populations and environmental responses, research across broader geographic areas is needed to assess the overall significance of deer browse as a priority for forest policy, management and restoration (Mladenoff and Stearns, 1993). Recent studies have successfully identified deer impacts at regional or sub-continental levels, focusing on the relationships between deer densities and forest species composition or structure (McWilliams et al., 2018; Russell et al., 2017; Bradshaw and Waller, 2016; McWilliams et al., 2015; Koh et al., 2010) and/or comparisons of vegetation development in deer exclosures to unprotected areas (Averill et al., 2018; Waller and Alverson, 1997). However, longitudinal studies extending farther back in time, especially to periods when deer populations had not yet reached current levels, are generally lacking and/or limited to the rare locations where quantitative historical understory data are available (Hale et al., 2008; Rooney and Dress, 1997; Whitney, 1984; Hough, 1965). Such baseline data are

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not only essential for determining the extent to which the forests of today have changed since that time (Magnuson, 2008), but for providing benchmarks or targets for forest restoration, stewardship and deer management.

Noteworthy exceptions to the dearth of long-term, regional studies of forest understory change are the ecological studies conducted in Wisconsin (Frerker et al., 2014; Rogers et al., 2008, 2009; Wiegmann and Waller, 2006; Rooney et al., 2004; Rooney and Rogers, 2004; Rooney and Waller, 2003) that built upon the historical data collected by John Curtis and colleagues from 1942 to 1956 (Curtis, 1959). These studies found major shifts in a wide range of plant community conditions from past to present, including declines in native species richness and density (Rooney et al., 2004; Rooney and Waller, 2003), decreased density or cover of preferred browse species (Rooney and Waller, 2003), shifts in native species composition (Wiegmann and Waller, 2006), and increased prevalence of exotic species (Wiegmann and Waller, 2006; Rooney and Rogers, 2004; Rooney and Waller, 2003). Deer browse was identified as one of the primary drivers of these changes; being either directly or indirectly responsible (Rooney and Waller, 2003). Comparisons of hunted and unhunted areas in northern Wisconsin, for example, found the greatest changes occurring in areas with higher deer densities (Rooney et al., 2004). Exclosure studies later confirmed the causal significance of deer in driving these changes, and documented associated changes to physical conditions as well, such as soils, light, nutrients and other factors (Sabo et al., 2017; Frerker et al., 2014). Frerker et al. (2014) concluded that deer browse was responsible for up to half of the variation in the long-term vegetation change observed. Other factors also contributed to these changes, especially in the more fragmented forests of southern Wisconsin, including stand age, patch size and surrounding landscape structure (Rogers et al. 2008, 2009).

New Jersey is likewise fortunate to have a rich tradition in quantitative, plant ecological research dating to the same time period as that of Curtis in Wisconsin, largely through the work of Murray Buell at Rutgers University (Reiners, 2016; Bormann and Pearson, 1975). With his students and colleagues, Buell conducted seminal research on the vegetation of New Jersey (Robichaud and Buell, 1973), and some of the earliest systematic, quantitative studies of forest ecology in the region (e.g., Buell and Wistendahl, 1955; Buell et al., 1954). For a quarter century from 1948 to 1973, a wealth of plant ecology research was conducted on forest structure and composition under his leadership, from descriptive studies of local forest preserves (Kramerm, 1967; Monk, 1959; Collins, 1956; Niering, 1950; McDonough, 1955) to investigations of broader ecological questions about the effects of slope, aspect and elevation (Good, 1965; Davidson, 1963; Ohmann, 1964, 1962; Hough, 1965; Hamilton, 1956, 1952; Cantlon, 1950), edge and patch size (Elfstrom, 1976; Wales, 1969), succession (Sulser, 1970; Niering, 1950; Bard, 1951), and soils and geology (Frye, 1975; Monk, 1959; Ohmann, 1964, 1962; Davidson, 1963; Pearson, 1960; Wistendahl, 1955).

Perhaps because they did not occur as a singular work, the value of this collective body of research for exploring regional forest change has largely escaped notice until now. Conducted under the guidance of Buell and his colleagues (e.g., Jim Quinn, Richard Forman), these studies employed nearly identical methods and metrics for sampling forest structure and composition; i.e., making it possible to assimilate them and provide a larger quantitative portrait of northern New Jersey forests during this time period. Because they sampled forests with a broad range of conditions, moreover, the cumulative data set is inclusive of a wide range of the variation occurring in forests and environmental conditions in the state. Indeed, Buell's larger-scale studies were explicitly intended to replicate Curtis's (1959) research in Wisconsin; i.e., to see if variation in forest conditions could be similarly identified across a continuum of environmental conditions in New Jersey (Reiners, 2016; Davidson and Buell, 1967; Buell et al., 1966). This data also happened to be collected prior to the explosion of both deer and

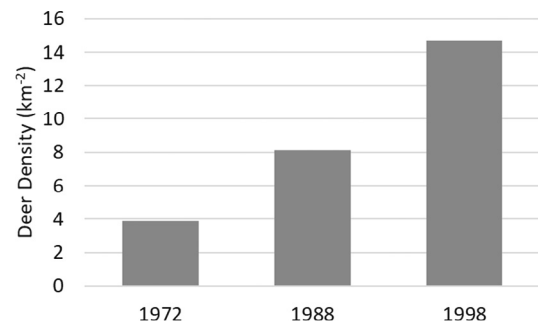


Fig. 1. Changes in deer population density in New Jersey. Adapted from NJDEP (1999) and SC and FoHVOs (2014).

non-indigenous plant populations in New Jersey (Fig. 1), thus providing the potential baseline data needed to understand the extent of impacts by deer and invasive plants in shaping forests today.

As in other areas, deer populations in New Jersey were nearly extinct by 1900 as a result of unregulated hunting, including commercial hunting which was banned at the end of the 19th Century (McCabe and McCabe, 1997). The implementation of stocking activities and improved game regulations by state biologists led to successful recovery such that by 1972, statewide deer populations had reached an estimated 3.9 km^{-2} on average (SC and FoHVOs, 2014); i.e., within the range of precolonial deer densities estimated by McCabe and McCabe (1997) of $3.1\text{--}4.2 \text{ km}^{-2}$. While these precolonial estimates are difficult to confirm, the effects on preferred browse species and forest structure that result when deer densities increase above 4 km^{-2} (Horsley et al., 2003; deCalesta and Stout, 1997; Alverson et al., 1988; Frelich and Lorimer, 1985; Behrend et al., 1970) suggest that they have biological merit as benchmarks for ecological study and/or management.

In the following decades, deer populations in New Jersey continued to climb to an estimated statewide density of 14.7 km^{-2} in 1998, with the highest regional densities of 30.1 km^{-2} occurring in northern-central New Jersey [NJ Department of Environmental Protection (NJDEP), 1999]. These estimates were derived primarily from deer harvest data, however, and may underestimate actual deer numbers, especially in suburban and other areas where hunting access is limited. Local deer populations in some of these areas, for example, have recently been observed at more than 77.2 km^{-2} (Williams et al., 2013; NJDEP, 1999). Because of the lower deer densities occurring at the time, the forest studies from 1948 to 1973 thus offer a useful background data set for investigating subsequent forest change from increased deer browse.

This study attempted to document the extent to which forest understories have changed in northern New Jersey since the mid-Twentieth Century, and combined observational and experimental evidence to further demonstrate the causal significance of deer in driving those changes. Evidence for alternative hypotheses explaining forest change, such as changing light regimes from historical logging, agriculture, fire or other disturbances (Mikan et al. 1994, Buell et al., 1954) and mortality from introduced pests and diseases (Holzmueller et al., 2010; Orwig and Foster, 1998; Good, 1965), were also considered in order to provide greater confidence in our conclusions (Nickerson, 1998; Mladenoff and Stearns, 1993; Chamberlin, 1965). By studying patterns across large spatial and temporal scales, I hope to contribute valuable information on the long-term effects of deer on regional forest change that are needed to inform forest policy and management in New Jersey and beyond.

2. Methods and study area

2.1. Study area

The area of study included the northern portion of New Jersey outside of the coastal plain (8080 km^{-2}). This region is comprised of

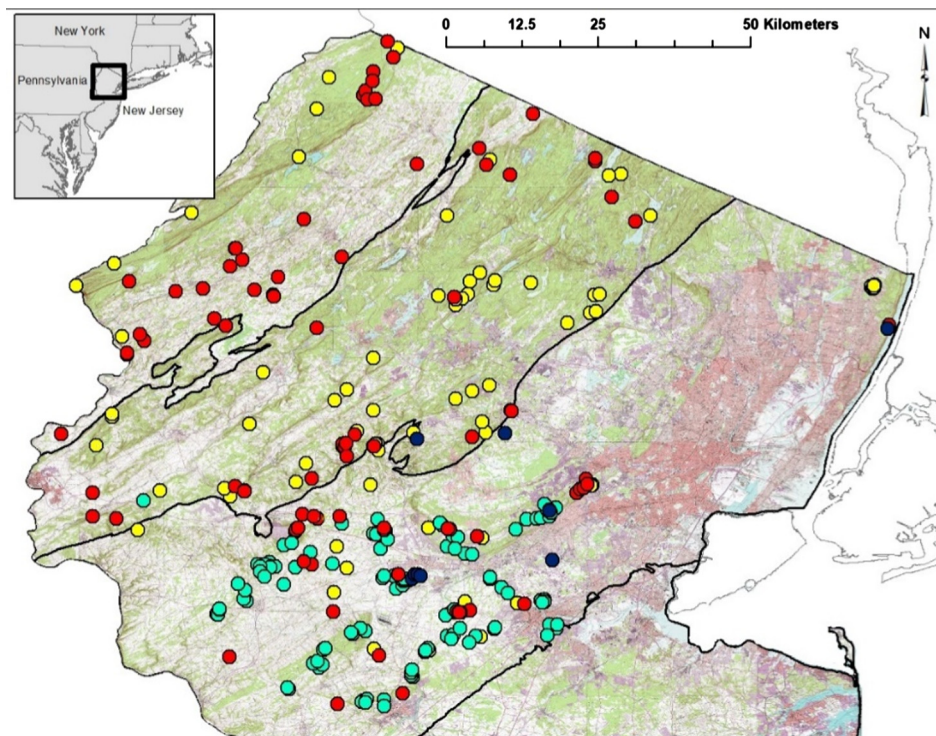


Fig. 2. Locations of study sites in northern New Jersey. Red dots indicate sites where both historical and present data were collected. Dark blue = exclosure locations, light blue = supplemental plots for local deer density surveys, yellow = additional historical study sites that were not included in this study. Basemap is USGS quad map, indicating forest cover (green), agriculture (white) and urban land cover (red/purple). Black lines indicate boundaries of physiographic provinces, including (from top left to bottom right) Ridge and Valley, Highlands, Piedmont and Coastal Plain. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

three physiographic provinces (Piedmont, Highlands, Ridge and Valley), which include a diverse range of topographic and geological conditions, forest cover and land use types (Fig. 2). Elevation above sea level ranges from approximately 30 m in the central Piedmont to 600 m in the northern Ridge and Valley. The human population of New Jersey is nearly 9.0 million (U.S. Census Bureau, 2013), and is distributed in the study area along a general density gradient from the east, adjacent to New York City, to the more rural and/or forested landscapes to the west and northwest. Forests of the region consist primarily of oak-hickory, mixed hardwoods, and northern hardwood types (Crocker et al., 2008; Robichaud and Buell, 1973).

2.2. Measuring changes in forest understories

A review of the scientific literature was conducted for all quantitative forest ecology studies pertaining to this region of New Jersey conducted prior to 1973. The collections of Rutgers University Library and other nearby institutions were also visited and searched for bound theses, dissertations and scientific reports to retrieve original data sets and site locations when these were not provided in the peer-reviewed literature. When data was only presented in graphical form, these were analyzed using ImageJ software (Rasband, 2018) to estimate the values indicated by bar or line graphs. Site locations were identified from original maps and site descriptions, historic maps of topography, park boundaries, and forest cover (Vermeule, 1899), and voucher specimens deposited at the Chrysler Herbarium at Rutgers University and other regional herbaria. Only studies of mature forest stands ≥ 3 ha in size were included.

A total of 22 quantitative forest ecological studies were identified for the time period 1948–1973 in northern New Jersey (Bard, 1951; Buell and Wistendahl, 1955; Cantlon, 1950; Collins, 1956; Davidson, 1963; Elfstrom, 1976; Frye, 1975; Good, 1965; Hamilton, 1952, 1956; Hough, 1965; Kramerm, 1967; McDonough, 1955; Monk, 1959; Niering, 1950; Ohmann, 1962, 1964; Pearson, 1960; Sulser, 1970; Tice, 1976; Wales, 1969; Wistendahl, 1955), which included data from 216 stands at 137 sites (Fig. 2). Of these, specific locations and quantitative data were available for 98 stands, including 76 with tree size class data,

50 with woody shrub and liana data, and 35 with herb cover. The remainder either did not present data in a compatible form for this study (e.g., continuum index values only), did not provide adequate information to identify specific site/sample locations, no longer were suitable for study due to conversion to other land uses, or were inaccessible in cases where permission to visit the sites could not be obtained.

Historical tree data was summarized as small seedlings (< 30 cm tall, < 2.5 cm), large seedlings (≥ 30 cm tall, ≤ 2.5 cm dbh), saplings (2.5–10 cm dbh), and trees (> 10 cm dbh), to be consistent with modern FIA regeneration terminology (McWilliams et al., 2015). Several historical studies, however, lumped two of these respective size classes together in their original data sets (Elfstrom, 1976; Good, 1965; Pearson, 1960; Ohmann, 1962). For these sites, their respective values were estimated by applying the respective size class ratios (e.g., large seedlings vs. small seedlings, saplings vs. large seedlings) from those sites where complete size class data existed ($n = 26$). The variation in these ratio patterns was first examined by plotting their distributions, to determine whether the mean, median or other quantile values of these ratios were most appropriate, and the strength of their linear relationships was assessed (R^2) in SAS-JMP 9.0. Individual size class values were then estimated for the sites where the data were combined, including 23 sites for small seedlings, 43 sites for large seedlings, and 20 sites for saplings. To determine whether these estimations altered or biased the overall historic data set, non-parametric one-way analyses of means were conducted, comparing historic data sets that excluded and included the estimated values.

For the 26 sites where complete size class data was provided, the large/small seedling ratios ranged from 0.6 to 3.5 (0.49 median; $R^2 = 0.14$), sapling/large seedling from 0.02 to 0.51 (0.09 median; $R^2 = 0.27$), and sapling/tree from 0.16 to 17.72 (median = 2.06; $R^2 = 0.12$) (Fig. 3). Because the distribution of these ratios across sites was highly skewed in each category (Fig. 3), along with the weakness of the linear relationship overall, the lower 10% quantiles of the ratios were used to estimate individual values for sites where these categories were combined, rather than using the median value, in order to be more conservative. These (10% quantile) ratios were 0.123 for large/small

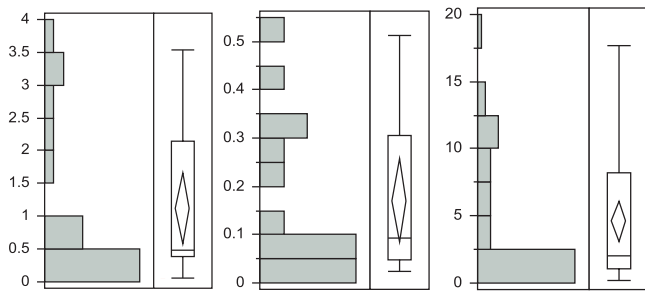


Fig. 3. Distribution of size class ratios used to estimate values from historical combined samples. Distribution diagrams include large/small seedlings (left), saplings/large seedlings (center) and saplings/trees (right). Box plots with median center line and mean diamonds provided for perspective.

seedlings (Elfstrom, 1976; Ohmann, 1962; Hamilton, 1952), 0.0295 for samples combining saplings/large seedlings (Good, 1965; Pearson, 1960), and 0.054 for saplings/trees (Good, 1965). When the resulting estimates from combined samples were included with the actual data sets of individual samples, they proved to be statistically similar for both small seedlings ($df = 1$, $X^2 = 0.9652$, $p = 0.3259$) and large seedlings ($df = 1$, $X^2 = 0.7271$, $p = 0.3938$) with the actual data sets alone, but not for saplings ($df = 1$, $X^2 = 5.2196$, $p < 0.0223^*$), which were significantly higher in the actual data compared to the actual + estimated data (Fig. 4). The median ratio values were less satisfactory, resulting in similar underestimates of saplings as well as major overestimates of large seedlings. The 10% quantile values therefore appeared to provide a more conservative method for disaggregating the combined values in the historical data set, which was consistent overall with the subset of historic data where the size class distributions were complete, but must be noted to potentially underestimate the number of saplings in the historic understory.

Data for present forest conditions were collected in summer of 2014–2018 by the author and trained field assistants from Raritan Valley Community College. A study design was developed to be consistent with historical studies in terms of sampling area, size class definitions, vegetation classification, and metrics. This consisted of three to four parallel 100 m transects spaced 20 m apart, with a minimum buffer of 20 m from any forest edge. Trees and saplings were measured in 10×10 m quadrats centered on the transect line, spaced 10 m apart and staggered by 10 m on adjacent transects, for a total of 1500–2000 m^2 sampling area spanning approximately one hectare of forest area overall (including buffers). Seedlings were recorded in two 0.5×2 m plots positioned lengthwise along the transect line at both the beginning and end of each 100 m^2 quadrat, for a total sample size of 30–40 m^2 per site. All historic studies used similar quadrat sampling along transects to measure tree density except for Kramer (1967),

Pearson (1960) and Ohmann (1964), who used point-quarter sampling. Total sampling area for most studies was 880–2500 m^2 . Samples collected on different years from Hutcheson Memorial Forest (Elfstrom, 1976; Sulser, 1970; Wales, 1969; Monk, 1959; Bard, 1951) were averaged first within and then between sample dates before integrating with the larger data set. Individual transects in McDonough (1955) were combined into four total samples according to spatial proximity and stand. Species nomenclature was converted to Gleason and Cronquist (1991), and data for *Fraxinus*, *Carya* and *Ulmus* were maintained at the genus level to be consistent with several historical studies (e.g., Buell and Wistendahl, 1955).

Shrubs, lianas and saplings were measured in terms of % cover using line intercept methods in each of the 100 m^2 quadrats described above. Percent cover of herbaceous species was recorded in each 1 m^2 seedling plot. Shrubs were defined as any species with multiple woody stems and/or average heights < 5 m; but *Hamamelis virginiana* was excluded from analyses due to inconsistencies in the historic and present data sets (McDonough, 1955) resulting from its varied growth form as either a tree or shrub. Studies that relied on shrub density (McDonough, 1955; Cantlon, 1950) or relative % cover (Niering, 1950) were excluded from the analyses, unless unoccupied space was also provided, allowing us to estimate actual cover.

Comparisons from past to present were made only for sites where both data were available, and included density of trees per size class (stems ha^{-1}), and total percent cover of saplings, shrubs, lianas and herbaceous plants (the aggregate cover of individual species, which may total more than 100). Data was also segregated for native and non-indigenous species to determine their relative contributions past and present. In order to maintain the independence of the data, statistical analyses were conducted of the change from present to past, using one-sided single-sample means tests to determine whether the rate of change differed from zero. In order to achieve greater symmetry between relative increases vs. decreases, the log ratio of change (i.e., fold-change) was analyzed instead of simple percent change or rate of change (Tornqvist and Vartia, 1985). All statistical analyses were done in SAS-JMP 9.0 using non-parametric Wilcoxon ranks and Kruskal-Wallis tests at confidence intervals of 0.95, providing signed-rank (R_o) test statistics and p-values to indicate significance. Variation in the data is provided in terms of standard error of the mean.

2.3. Effects of Deer: Observational and experimental evidence

In order to analyze shifts in species composition in relation to deer browse preference, tree species were classified according to Latham et al. (2005) as high, intermediate or low preference. Several modifications were made based on local observations (Kelly pers. obs.), including “low” designations given to *Fagus*, *Betula*, *Sassafras*, and *Juniperus*, and “intermediate” designations given to *Tilia* and *Liriodendron*,

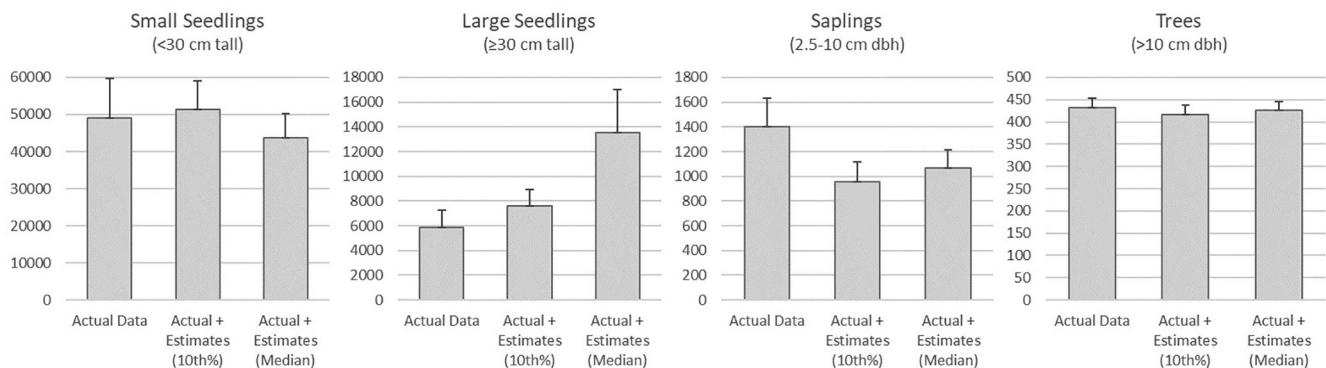


Fig. 4. Comparison of historical baseline data sets. Comparisons of possible baseline historical datasets, including only original size class data, and original data plus estimations of individual values when size classes were combined by original authors. Estimations are based on 10% quantiles and medians of size class ratios, respectively. Bars represent stems ha^{-1} with error (SE).

which are also supported by other studies (Miller et al., 2009; Benner, 2007; Asnani et al., 2006; Petrides, 1941). Changes from past to present were measured using one-sided single-sample means tests to determine whether the average change differed in either direction from zero. All statistical analyses were done in SAS-JMP 9.0 using non-parametric Wilcoxon ranks and Kruskal-Wallis tests at confidence intervals of 0.95.

To better determine the relationships of saplings to deer density, a total of 89 additional forest plots were established in 24 clusters to provide greater local sampling intensity and compare average sapling numbers to local deer densities. Plots followed the same sampling design as described above. Plot clusters were typically > 3 km apart with sites within clusters being < 1 km apart. Because deer density estimates based on harvest data are known to underestimate deer densities in suburban areas where hunter access is limited, deer surveys were conducted using road-based spotlight techniques to gain more accurate local estimates (Drake et al., 2005). Surveys were conducted from late March through early May in 2016–2018, which provides both the most accurate (leaf-off) and most conservative (post-hunting, pre-birthing) estimates of the year. Based on the average winter range size of 0.3–2.25 km² in suburban areas (Williams et al., 2008; Kilpatrick et al., 2001; Tierson et al., 1985), surveys were conducted on all roads < 40 mph within 1.2 km of forest study sites, in order to identify all deer that had a reasonable likelihood of using those forest patches at this time of year. Surveys were conducted from 9:30 PM, more than one hour after dark, until approximately 2 AM, and only with winds < 15 mph and no precipitation. Deer were counted along each survey route using high-powered hunting flashlights (Wicked Lights W403IC), and the limits of the search area to either side of the vehicle was recorded using laser rangefinders every 0.2–0.3 km. A minimum of two samples were collected for each route, on two separate nights with a minimum separation of ten days. Plot-based sampling (Jester and Dillard, 2010) was used to calculate density; dividing the number of deer by the total search area. Given the limited visibility of forest patches and other large tracts of land with no road access, the survey results likely underestimated deer totals in these areas. The maximum number of deer observed per route was consequently used in the analyses rather than the average. Our spotlight survey data set was also supplemented by contemporaneous deer density data collected by others in the region using similar methods (Williams et al., 2013, SC and FoHVOS, 2014, T. Almendinger unpubl. data). The average number of saplings from each cluster was then plotted against maximum observed deer density for that cluster and the line of fit was log-transformed for both x and y variables in JMP 9.0.

Experimental data on deer relationships was collected from nine deer exclosures at six locations. Exclosures were categorized by age, including four (n = 2), seven (n = 2), and 11–20 (n = 5) years old. Most exclosures were 0.5–3 ha in size. The two largest exclosures (259 and 10 ha) included four and two subsamples, respectively, and were amongst the oldest (11–20 years). Comparisons of understory response to unprotected forests (past and present) were made with only the oldest exclosures to allow time for understory development (Freker et al., 2014; McGarvey et al., 2013). Seedling heights following McWilliams et al. (2015) were also recorded in a subset of exclosure plots and ten unprotected sites chosen at random. These data were collected in 2 × 2 m plots at the beginning and end of each 100 m² quadrat along the transect line.

Although stewardship activities such as invasive plant removal have occurred in several of the exclosures, care was taken to collect data in areas not subject to these activities. The exclosures have not been entirely free from deer influence, as several have been subject to occasional browse when fencing was damaged, and the largest exclosure contained a resident deer population since 2012, maintained at approximately 3.9–6.2 km⁻² by annual culling (T. Almendinger pers. comm.). The largest exclosures (4–259 ha) all have recreational trails, and are therefore exposed to possible human disturbances as well. Two-sample mean comparisons of tree density and total % cover for

understory vegetation between the exclosure and historical and present data sets were conducted in SAS-JMP 9.0 using non-parametric Wilcoxon ranks and Kruskal-Wallis tests at confidence intervals of 0.95. Chi-square and p-values were reported to indicate significance.

2.4. Evidence of other causal factors

In order to determine whether changes in light availability affected historical vs. present tree densities, tree species composition was classified according to shade tolerance following Burns and Honkala (1990). Evidence of prior logging, fire, and other disturbances was gathered from the original studies, which often directly addressed these issues. Other evidence of historical agricultural use or clearcutting was gathered by examining aerial photographs from 1930 for each site (NJ Office of Information Technology, 2009) and the Vermeule (1899) forest cover map for northern New Jersey. Data for select tree species (*Ulmus americana*, *Cornus florida*, *Castanea dentata*, *Tsuga canadensis*) affected by introduced host-specific pest or disease species were also analyzed to determine whether they exhibited major declines and whether their removal from the data set reduced the significance of overall declines (Orwig and Foster, 1998). Because field data was collected prior to major local infestations of emerald ash borer, beech bark disease, and other pests, no other species (e.g., *Fagus grandifolia*, *Fraxinus* spp.) were included as part of this analysis.

3. Results

3.1. Changes in forest understories

Major declines in tree densities and recruitment were observed from past to present according to size class. The historic data set (n = 62) included an average of 51,375 (± 7556) small seedlings ha⁻¹, 7626 (± 1315) large seedlings ha⁻¹, 957 (± 159) saplings ha⁻¹, and 416 (± 22) trees ha⁻¹. The same stands in 2014–2018 had an average of 31,568 (± 3579) small seedlings ha⁻¹, 1539 (± 205) large seedlings ha⁻¹, 258 (± 26) saplings ha⁻¹, and 342 (± 13) trees ha⁻¹ (Fig. 5). This amounts to declines of –39% for small seedlings (df = 61, $R_o = -101.5$, $p = 0.2353$), –80% for large seedlings (df = 61, $R_o = -808.5$, $p < 0.0001^*$), –75% for saplings (df = 55, $R_o = -448.0$, $p < 0.0001^*$), and –18% for trees (df = 55, $R_o = -219.0$, $p < 0.0369^*$). A total of 84% of sites sampled exhibited declines for large seedlings, with half the sites declining by –80% or more, and 66–69% of sites declining in each of the other size classes. Half declined by –48% or more for saplings, and –28% and –6% for small seedlings and trees, respectively.

Major declines in total % cover were also observed in all other categories of native understory vegetation measured (Fig. 6). Native shrubs declined an average of –72% (df = 49, $R_o = -589.0$, $p < 0.0001^*$), herbs –76% (df = 34, $R_o = 248.5$, $p < 0.0001^*$), and saplings –91% (df = 27, $R_o = -199.0$, $p < 0.0001^*$). Although average native liana cover declined by –46%, these changes were not statistically significant (df = 49, $R_o = -83.0$, $p = 0.1692$). Half the sites declined by –87% or more in the case of native shrub cover, and –76% in the case of native herb cover. The median change for native lianas was 7%.

Major increases in exotic plant species were also observed, including 40× increases for exotic shrubs (df = 49, $R_o = 447.5$, $p < 0.0001^*$), 11× increases for exotic lianas (df = 49, $R_o \geq 270.5$, $p < 0.0001^*$) and 5× increases for exotic herbs (df = 34, $R_o = 174.0$, $p < 0.0001^*$). These changes in total native and exotic species cover led to major shifts in overall species composition per site (Fig. 6). Whereas sites were ≥95% native in each category in the historical data set, shrubs and lianas were predominately invasive (54% each) today (Fig. 7). Although native herb cover maintained its dominance, invasive herbs increased to 22% of the total. Although herbarium specimens and tree structure data show exotic species to be present at many historic sites,

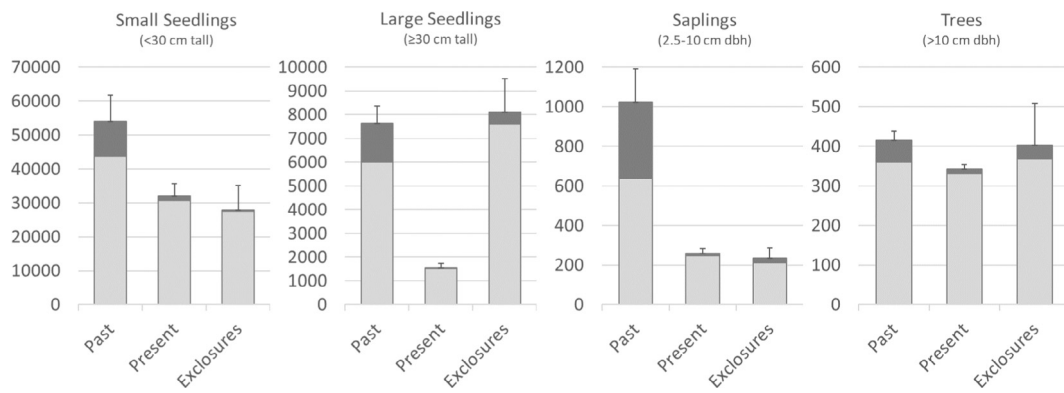


Fig. 5. Changes in the size class structure of trees in northern New Jersey. Graphs show densities of small and large seedlings, saplings, and trees in 62 stands from past (1948–1973) to present (2014–2018) and in five 11–20 yr-old deer exclosures (2016–2018). Bars indicate mean # stems ha^{-1} , with error bars (SE). Dark portions of bars indicate proportions of trees represented by *Cornus florida*, *Tsuga canadensis*, *Castanea dentata*, and *Ulmus* spp., which also experienced declines from introduced pathogens.

sapling cover for individual species was not provided in the historical data sets, preventing comparisons between native and invasive species in this category.

3.2. Effects of Deer: Observational and experimental evidence

The observational and experimental analyses strongly suggest that deer browse was the primary causal factor driving the declines in tree recruitment over time. Major shifts in species composition were observed with regard to browse preference (Fig. 8), with significant increases in all categories for less preferred browse species ($df = 61$, $R_o = 457.5$, $p \leq 0.0005^*$) and major decreases observed for highly preferred species ($df = 61$, $R_o = -447.5$, $p < 0.0004^*$). The large seedling and sapling categories, which experienced the greatest numerical declines from past to present, also exhibited by far the greatest changes, with 136% and 156% increases in low browse preference species, respectively, and –58% and –68% decreases for highly preferred browse species.

Spotlight surveys were conducted in 18 locations over 111 miles of roads, with data for 6 additional nearby sites taken from the literature (SC and FoHVOs, 2014; Williams et al., 2013) and T. Almendinger (pers. comm.). Deer densities averaged 46 ± 6.8 deer km^{-2} (149 deer km^{-2} max) and large seedling numbers averaged 1320 ± 483 stems ha^{-1} . Comparisons of large seedling numbers to local deer densities (Fig. 9) found a strong relationship when the axes were log transformed ($R^2 = 0.47$). Only areas with aggressive deer management programs had deer densities lower than 30 km^{-2} and/or large seedling numbers over 2200 ha^{-1} . Half the study sites had 403 large seedlings ha^{-1} or

fewer.

Deer exclosures 11–20 years in age showed 86% increases in large seedling numbers ($8101 \pm 1400 \text{ ha}^{-1}$) compared to unprotected sites ($df = 1$, $Z = -3.59084$, $p = 0.0003^*$), rising to levels nearly identical to the historic average ($df = 1$, $Z = -1.34806$, $p = 0.1776$) (Fig. 10). The numbers of saplings ($267 \pm 31 \text{ ha}^{-1}$) were not statistically different from historic sites ($df = 1$, $Z = 1.65641$, $p = 0.0976$); however, they were clearly more comparable to unprotected present-day samples ($df = 1$, $Z = -0.61803$, $p = 0.5366$) than historic, suggesting that full recovery of this understory layer may take more than two decades on average. Small seedlings ($30,088 \pm 6454 \text{ ha}^{-1}$) and trees ($397 \pm 108 \text{ ha}^{-1}$) were also similar to both historic and present data sets ($df = 1$, $Z \geq -0.72334$, $p \geq 0.4695$).

Clear positive trends in large seedling numbers and heights were observed in exclosures over time (Fig. 10). Major increases occurred in large seedling numbers every 3–4 years, to $2151 (\pm 1389) \text{ ha}^{-1}$ in the 4 yr exclosures, and $3902 (\pm 1438) \text{ ha}^{-1}$ in the 7 yr exclosures, representing increases of 40% and 154% over unprotected forests, respectively. Major increases were also observed in the abundances of all size classes of seedlings $> 15 \text{ cm}$, with the largest size classes ($> 1.5 \text{ m}$) being present only in the oldest exclosures in large numbers. The 7 yr exclosures were excluded from this analysis, as recent deer intrusion from downed fencing led to significant reduction in larger seedling heights. Major increases (14x) were also observed in large seedling cover in 11–20 yr exclosures compared to unprotected sites. The proportions of large seedlings represented in 11–20 year old exclosures was nearly identical to the historic data, with 25% low browse species and 57% species of high browse preference, compared to 29%

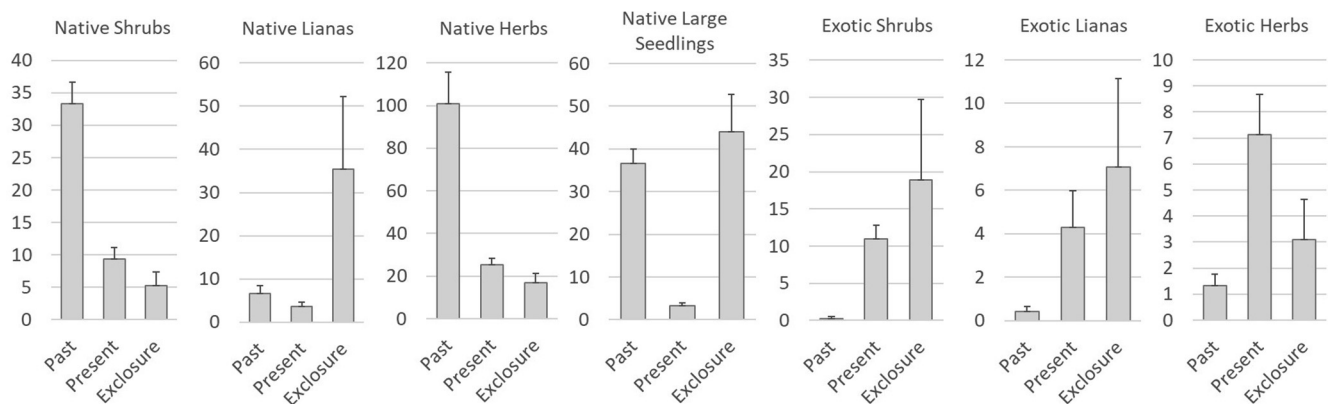


Fig. 6. Changes in percent cover of native and exotic understory vegetation in northern New Jersey. Graphs show total cover of shrubs and lianas ($n = 50$ stands), herbs ($n = 35$) and large seedlings ($n = 62$) from past (1948–1973) to present (2014–2018) and in five 11–20 yr-old deer exclosures (2016–2018). Bars indicate mean % cover with error (SE).

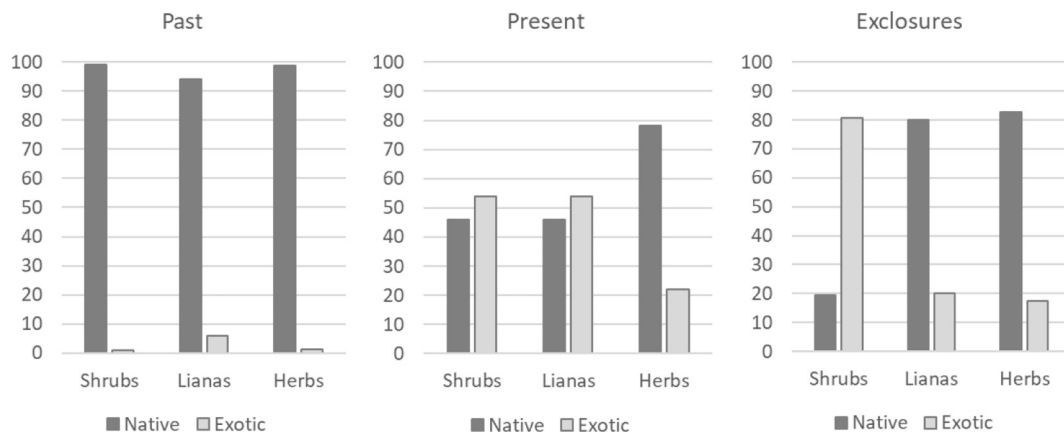


Fig. 7. Changes in percent composition of native and exotic plant species in forest understories in northern New Jersey. Graphs show average proportion of total cover represented by native and exotic species for shrubs, lianas and herbs from past (1948–1973) to present (2014–2018) and in five 11–20 yr-old deer exclosures (2016–2018).

and 55% (respectively) in the historic data (Fig. 8).

Positive trends were observed on average for both native and invasive lianas and invasive shrubs in exclosures > 10 years old (Fig. 6), with native lianas increasing 10x and invasive lianas and shrubs both doubling. None of these increases were statistically significant, however, due to variation and small number of exclosures, with the greatest differences being for native lianas ($df = 1$, $X^2 = 2.5859$, $p = 0.1078$). Herb cover decreased in exclosures for both natives (−33%) and invasives (−49%), likely due to increased shade resulting from the dramatic increase in large seedling cover. Positive trends in overall species composition were also observed for lianas and herbs (Fig. 7), with native lianas rising to dominance over invasives, and native herbs maintaining their dominance. Invasive shrubs, however, increased their dominance in exclosures compared to unprotected sites.

3.3. Evidence of other causal factors

The evidence available on the disturbance history of the study sites as well as the shade tolerance of species composition suggests that the higher numbers of large seedlings and saplings occurring in mid-Twentieth Century forests was not the result of increased light levels compared to the present, and/or histories of disturbance (logging, agricultural use, fire, etc.). Because the historical studies were interested in characterizing high quality, ecologically-intact forests, most sites were selected specifically to avoid areas with recent histories of

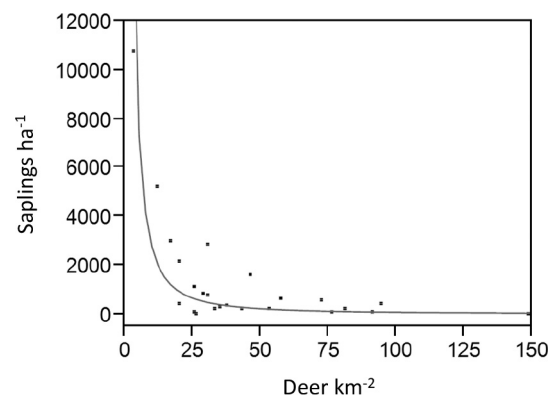


Fig. 9. Relationship of average large seedling density to deer density in northern New Jersey in 2014–2018. Data on average deer density (deer km^{-2}) was collected by spotlight surveys on all roads within 1.2 km of 24 forest areas, and compared to average large seedling density (stems ha^{-1}) in each area. Linear regression of log-transformed data yielded an R^2 value of 0.47.

disturbance. Davidson (1963), for example, used minimum of 60 yrs since disturbance (logging, fire) as a criterion for selecting sites, and several sites had no history of disturbance since colonization based on tree ring data and other records (Pearson, 1960; Buell, 1957; Buell and Wistendahl, 1955). Aerial imagery and historic forest maps found only

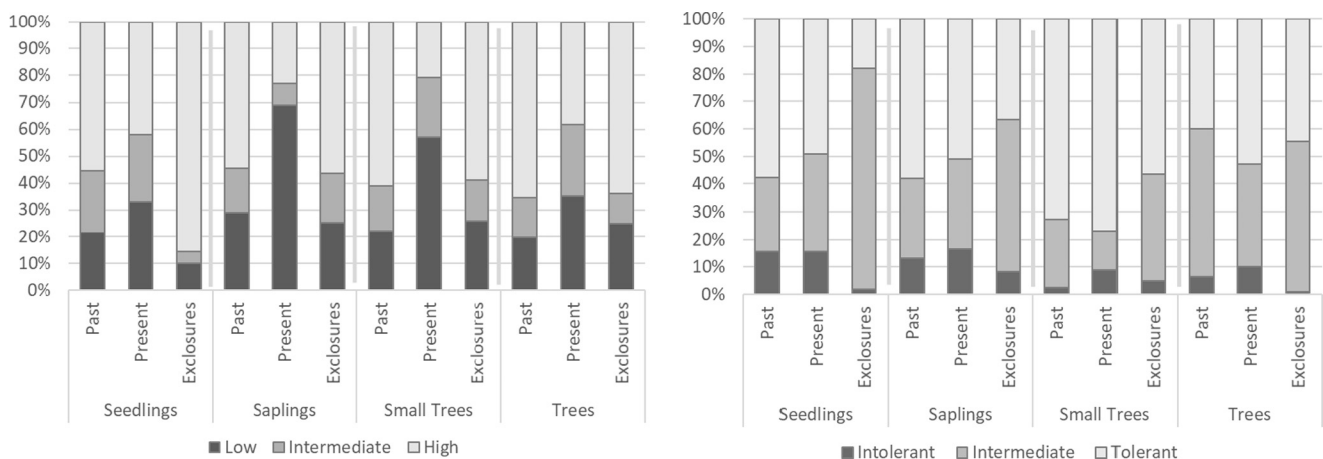


Fig. 8. Changes in proportions of tree species in different size classes according to deer browse preference (left) and shade tolerance (right) in northern New Jersey. Graphs compare proportions of species in each category for small and large seedlings, saplings, and trees in 62 stands from past (1948–1973) to present (2014–2018) and in five 11–20 yr-old deer exclosures (2016–2018).

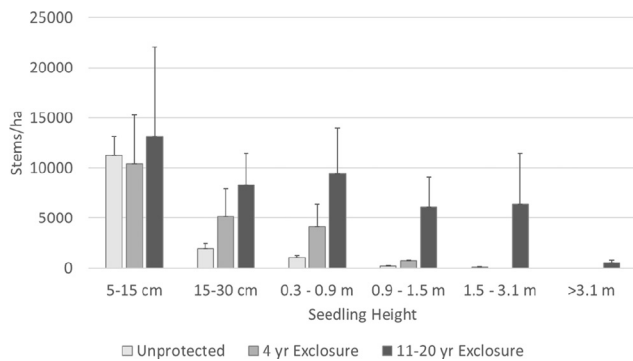


Fig. 10. Relationship of seedling height classes to exclosure age in northern New Jersey in 2016–2018. Exclosures include two 4 year-old exclosures, five 11–20 year-old exclosures, and 10 unprotected sites.

one site to have any evidence of agriculture (Frye, 1975), which was 60–70 years prior. The most recent cases of disturbance were in Pearson (1960), who identified minor disturbance 15 years earlier at one site, with selective cutting of cedars and dead trees for posts and firewood, and prior selective cutting approximately 30 years earlier at four other study sites. The remainder had no evidence of logging or other major disturbance in the historical record, and no signs of disturbance during site visits in 2014–2018 except for minor occasional cutting of trees for firewood. Further evidence of this lack of canopy disturbance history comes from the species composition data, which shows no significant changes from past to present in the shade tolerance of trees in the understory (Fig. 8). Trees (> 10 cm dbh), however, did exhibit 11% increases in shade tolerant species on average ($df = 54$, $X^2 = 393.0$, $p = 0.0003^*$). If significantly more light was available in historical forests compared to the present, there would have been much greater differences reflected in the data sets.

Analysis of the densities of *Cornus florida*, *Tsuga canadensis*, *Ulmus americana*, and *Castanea dentata* in the historic data sets supported the possibility of tree mortality from infectious diseases contributing to overall tree declines. These species represented substantial proportions of each size classes of trees (Fig. 5) and suffered greater cumulative declines (–80 to 98%) from past to present than forest changes overall (–18 to 80%). When these species were removed from the data sets, the observed overall declines in the trees (> 10 cm dbh) were no longer significant ($df = 55$, $X^2 = 11$, $p = 0.5353$), which was also true when *C. florida* or *T. canadensis* were removed individually. However, the declines in large seedlings ($df = 61$, $X^2 = -761.5$, $p < 0.0001^*$) and saplings ($df = 55$, $X^2 = -205$, $p = 0.0474^*$) remained significant, and no change was observed in small seedlings ($df = 61$, $X^2 = -49.5$, $p = 0.3627$). Mortality from pests and diseases was therefore not sufficient to explain the scale of overall decline in tree recruitment from past to present. *Cornus florida* comprised the greatest proportion of affected species, representing 15–29% of total small and large seedlings and saplings in the historic data set as a whole, compared to 2–5% for *Tsuga canadensis*, and 0.3–3% for *Ulmus* spp. and *Castanea dentata*. *Cornus florida* and *T. canadensis* comprised 6–7% of medium and large trees, respectively, compared to < 1% for *C. dentata* and *Ulmus* spp. Given their small proportions in the historic data set, the declines of the latter two species from chestnut blight and Dutch elm disease likely took place prior to 1948–1973 in northern NJ. While it is possible that the loss of these canopy species contributed to the greater amount of tree regeneration observed at that time, this would have resulted in greater proportions of shade intolerant species appearing in those size classes, which was not found to be the case as described above (Fig. 8). The loss of *T. canadensis* was also much more significant in the subset of locations where it was abundant than in the data set as a whole. This species was present at 23% of the historic sites, and represented 20% or more of canopy tree abundance at six of them (10%).

4. Discussion

Major regional declines in native understory vegetation and shifts in plant community composition have occurred since the mid-Twentieth Century in northern New Jersey forests. Chronic browse from overabundant white-tailed deer was the primary cause of decline in recruitment, with close relationships found between large seedling numbers and local deer densities, and shifting species composition according to browse preferences. Most convincing was the experimental data from long-term exclosures, showing full recovery of large seedling densities to historic levels, the return of highly preferred browse species to historic proportions, and successful survivorship and growth of seedlings over time. Although no increases were yet observed in saplings, the height trajectories of larger seedlings indicated their recovery is imminent as well. Given the wide range of forest conditions included in this study, the decimation of tree recruitment and other understory vegetation by deer clearly represents a priority for regional forest management in northern New Jersey.

These problems are not limited to New Jersey, moreover, but are part of broader trends occurring throughout many other areas of the region and the world (Russell et al., 2017; McWilliams et al., 2018, 2015; Bradshaw and Waller, 2016; Frerker et al., 2014). In a sub-continental study of browse impacts from the Great Plains through the northeast, for example, McWilliams et al. (2018) found widespread impacts by deer, with a 59% probability of moderate or high levels of browse overall, and 79% for the Mid-Atlantic region in particular. Analysis of seedling densities from Forest Inventory Analysis plots across roughly the same area (Russell et al., 2017, Fig. 2) showed some of the lowest levels to occur in the Mid-Atlantic and the Upper Midwest, where deer densities have been similarly elevated for decades (Bradshaw and Waller, 2016; Frerker et al., 2014). Similar patterns indeed have occurred in many other parts of the world, with ungulate populations increasing in response to the extermination of natural predators, increased forest fragmentation, and other factors that favor their growth (Ripple et al., 2010).

While the geographic scale of overabundant deer populations (McWilliams et al., 2018) presents a major challenge for ecosystem recovery, it also presents opportunities for local management. Unlike many other factors impacting forests, such as acid rain, climate change, and pest or disease outbreaks, it is relatively feasible to address the problem of overabundant deer at the local level. Evidence from deer exclosures in numerous studies have repeatedly demonstrated improvements in forest regeneration and other environmental conditions (Averill et al., 2018; Sabo et al., 2017; Frerker et al., 2014; McGarvey et al., 2013). Exclosures, however, are not a realistic solution to forest restoration at the landscape, regional or sub-continental scales at which these problems are occurring (McWilliams et al., 2018; Russell et al., 2017). The only alternatives that appear to have the possibility of providing comparable benefits at these larger scales are deer management through predator reintroductions (Ripple and Beschta, 2012), intensive hunting programs (Williams et al., 2013; Rojo et al., 2010; Rooney et al. 2004a; Brown et al., 2000), or allowing large forest blocks to succeed to late successional stages (Alverson et al., 1994). While all have their costs and challenges, they are far lower than the costs of inaction, which include not only continued forest and other ecosystem decline, but deer-vehicle collisions, disease transmission, agricultural damage and other costs to society (Conover, 2011; Côté et al., 2004). Not all hunting programs are effective at achieving these goals, however, with those focused on recreational hunting being insufficient to reduce deer densities below the necessary thresholds for ecosystem integrity or public safety (deCalesta, 2017). Research is needed to determine the extent to which different types of hunting programs translate into improvements of these kinds, and the policies and incentives that are most effective at achieving these goals.

The methods used in this study and others (Russell et al., 2017; McWilliams et al., 2015) appear to offer valuable tools for gauging the

effects of deer management and/or other techniques for forest restoration on tree regeneration. Of particular importance in this regard is the discrimination between smaller size classes of trees in order to detect the effects of deer at different temporal scales. Tree seedlings < 30 cm tall, for example, are less valuable indicators of chronic browse, as they are replenished annually from the canopy trees above and are inherently variable due to weather, masting and other factors associated with annual seed production (Abrams, 2013). They are also typically first browsed by deer in the late fall/winter after their first growing season (Bradshaw and Waller, 2016); i.e., after the time when vegetation studies are typically conducted, and are therefore less likely to exhibit impacts from local deer populations. In contrast, the New Jersey enclosure data suggest that larger seedlings (> 30 cm) spend more than ten to fifteen years in this size class on average, and are therefore a more sensitive and useful indicator of deer browse. When seedling size classes are instead lumped together, the far more abundant small seedlings mask the numbers of large seedlings and with it any signs of excessive browse by deer. The finer-scale seedling height classifications of McWilliams et al. (2015) provided further value in illustrating the variable sensitivity of specific classes to browse, but are also substantially more time-consuming to collect than simpler classifications. Given its lack of recovery in the 11–20 year old enclosures, the sapling size class (2.5–10 cm dbh) also appears to provide a valuable indicator of longer-term deer browse, on the order of multiple decades (Bradshaw and Waller, 2016). Conversely, it also provides useful perspective about the long-term commitments needed for recovery, with complete recovery of saplings likely taking more than 20–30 years.

Ultimately, the absence of a background data set in most locations precludes the precise determination of recruitment or other deficiencies existing in forest understories today as a result of deer or other causes (Magnuson, 2008). In this regard, the baseline historical data compiled in this study provided invaluable perspective for identifying the extent to which deer and other factors have altered forest structure and composition since the mid-Twentieth Century. While quantitative data for forest understories are relatively rare at the regional level, it is possible that other data sets exist in archives and unpublished theses as they did in this study, awaiting to be similarly compiled. These baseline data are important not only for chronicling forest change, but for setting targets and monitoring the success of restoration and/or forest or deer management. Knowing the average density or % cover of young trees, shrubs, or herbs that were present in the landscape prior to deer population explosions can help determine the success of deer enclosures or other deer management, for example, as well as appropriate planting densities for active restoration. It is also valuable for determining the relative costs of different strategies of forest restoration (i.e., artificial planting vs. natural recruitment via enclosures or hunting) and the feasibility of restoring forests to their former densities of trees or other native vegetation.

In addition to reduced densities of trees in the understory, major declines in % total cover were observed in all other native understory vegetation types as well, including native shrubs, herbs, and lianas, along with concomitant increases in exotic species. However, while deer browse was certainly a major factor in their declines, the lack of a positive response of native shrubs and herbs in the deer enclosures indicates that other factors were at work in driving their declines and/or inhibiting their recoveries. Such confounding factors include seed source and dispersal limitations, site history, edge effects, and competition with exotic invasives (Ward et al., 2018; Beasley and McCarthy, 2011; Rogers et al., 2008, 2009; Johnson and Klemens, 2005). Unlike the seed sources for trees and lianas, which are continually replenished from the canopy above, herbs and shrubs must rely on seed banks and/or dispersal to replenish their numbers. These are much more vulnerable to depletion by chronic browse and/or effects of fragmentation. All of the 11–20 year enclosures studied in New Jersey, for example, were located in the Piedmont, where the history of disturbance, development

and forest fragmentation was the greatest (Russell, 1988; Lathrop et al., 2016). The long-term effects of deer may have been so severe that greater lengths of time or active vegetation management are needed to achieve full recovery of native understory vegetation in these enclosures (Pendergast et al., 2016). When the extremely high numbers of deer (> 77 deer km⁻²) were first removed from the largest enclosure (259 ha) in this study, for example, biologists found a total of only two individuals of *Viburnum acerifolium* remaining (T. Almendinger pers. comm.); i.e., greatly limiting available seed sources to support the recovery of this species (which now numbers several dozen) compared to other, much more prevalent invasive shrubs in the area. The continued decline observed in shrubs and herbs in enclosures may therefore have been due to interacting effects between competing understory vegetation types upon release from browse; e.g., increased competition between natives and exotic species in the case of shrubs (Ward et al., 2018), and increased shading of both native and exotic herbs resulting from the dramatic increase in sapling densities above (Sabo et al., 2017; Frerker et al., 2014). Lastly, it is also worth noting that total % cover may not be a sufficiently sensitive metric for identifying the effects of deer in these understory layers, given the differences in individual species responses to deer browse that results in some species increasing over time (Averill et al., 2018; Rooney, 2009; Wiegmann and Waller, 2006).

Confounding factors were also likely at work in the case of understory tree densities. Substantial support was gained for the possibility of mortality from introduced pests and diseases being a significant contributing factor to tree declines from past to present in New Jersey, with vulnerable species declining at far greater rates than the average. However, the loss of these species was not sufficient to explain the scale of observed changes overall, as the declines remained significant when they were removed from the data set. The species most affected since the mid-Twentieth Century (*Tsuga canadensis*, *Cornus florida*), moreover, are also highly preferred deer browse species and their moderate response to enclosures suggests that deer were also a contributing factor to their decline to some degree. Other possible causes of the observed declines in tree recruitment were eliminated entirely, however, including the possibility of decreasing light availability due to changing disturbance regimes (e.g., logging, fire, agriculture). No major increases in shade tolerance or decreases in shade intolerance were observed over time in understory size classes, and the historical forest studies explicitly focused on higher-quality, older forests that were free from recent disturbance. There is therefore no evidence to suggest that the greater densities of understory tree densities in the past were due to increased light resulting from human or other disturbance. This offers an important lesson for forest management, as it indicates that greater regeneration may be obtained not only by canopy thinning but by successful deer management. Indeed, in the absence of the latter, the former may be counterproductive, serving only to increase forage for already elevated deer populations rather than yielding effective recruitment.

The bias in the historic New Jersey data set towards older, less disturbed forests with relatively intact soils and community assemblages is another important limitation of this study. Conspicuously lacking are samples collected from the extensive forested areas occurring on post-agricultural soils in New Jersey, which resulted from the abandonment of farming practices in the region in the early 20th Century (White et al., 1990; Russell, 1988). Further research is needed to document the conditions of these younger forests, and the degree to which they have been impacted by deer and exotic plant species in comparison, as well as by soil degradation, invasive earthworms, and other related factors (Davalos et al., 2015; Dyer, 2010; Nuzzo et al., 2009; D'Orangeville et al., 2008; Singleton et al., 2001).

As drastic as the documented changes to forest understories in New Jersey appear to be, it is important to note that the methods used to estimate historic forest conditions in this study were highly conservative, and therefore likely underestimate the severity of forest

decline. Not only did the study focus on older, more intact forests that are less vulnerable to long-term degradation, but it utilized highly conservative quantitative methods that may have underestimated the baseline historic densities of understory trees. Furthermore, some of the forests in the historic studies may have already been subject to elevated browse pressure, reducing the baseline from which subsequent changes were measured. Although the estimated statewide deer density during the historic 1948–1973 study period (≤ 3.9 deer km^{-2} , Fig. 1) conveniently corresponds with both pre-colonial deer densities (McCabe and McCabe, 1997) and biologically relevant thresholds (deCalesta and Stout, 1997; Alverson et al., 1988; Frelich and Lorimer, 1985; Behrend et al., 1970), regional variation in deer populations in New Jersey suggest that numbers in northern NJ were likely higher at the time, given that the southern pine barrens region of the state typically supports much lower densities of deer (NJDEP, 1999). Record deer populations were anecdotally reported for the far northern parts of the state in the 1950 (NJDEP, 1999); moreover, and concerns about local deer browse were noted by forest ecologists as early as the mid-1960 (Kramerm, 1967). Several studies were initiated in the early 1970 to study the effects of deer browse, with Tice (1976) and Reynolds (1980) reporting heavy browse affecting hemlock and red maple growth and survival in some areas.

The severe declines observed in nearly all forest understory layers since the mid-Twentieth Century clearly present a major challenge for forest stewardship and restoration in the future. Continuation of these trends will result in the further deterioration of the many benefits these forests provide, including biodiversity, wildlife habitat, carbon sequestration, soil and water quality, and economic and aesthetic values (Shifley and Moser, 2016). The severe long-term depletion of the smaller size classes of trees may even threaten the survival of the forests themselves, leading to a failure of younger trees to adequately replace older, larger trees as they die off. This most extreme outcome of these processes is already occurring in places in New Jersey, particularly in small forest fragments with greater exposure to disturbance, where large scale mortality from storms or pests and diseases is resulting in their conversions to thickets of invasive shrubs and lianas or other vegetation types (Johnson and Klemens, 2005). Greater attention to these matters is urgently needed if further declines to our forest conditions are to be avoided.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.04.050>.

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