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# Subcontinental-Scale Patterns of Large-Ungulate Herbivory and Synoptic Review of Restoration Management Implications for Midwestern and Northeastern Forests

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## ABSTRACT

Browse of forest understory vegetation by deer and other large ungulates alters ecosystem processes, making it difficult to regenerate forest land in herbivory-stressed areas. Seventy years ago, Aldo Leopold identified problem areas in the United States where overpopulation of white-tailed deer (*Odocoileus virginianus*) was likely to lead to overbrowsing of nutritive plants. Species of plants with little or no nutritive value would thereby gain a competitive advantage. Recent measurements of browse impacts on regionwide forest inventory plots in the midwestern and northeastern United States provide the opportunity to review the work of Leopold and others. A visualization of the probability of browse impact levels that warrant consideration during regeneration planning is presented for comparison to historical maps.

Currently, 59 percent of the 182.4 million acres of forest land inventoried in the Midwest and Northeast was estimated to have moderate or high browse impacts. The Mid-Atlantic region had the highest proportion of forest land with moderate or high browse impacts (79 percent). The oak/hickory (*Quercus*/*Carya*) and maple/beech/birch (*Acer*/*Fagus*/*Betula*) forest-type groups each had percentages of forest land with moderate or high impacts above the regional average, 69 percent and 65 percent, respectively. The problem areas described by Leopold and others persist and new areas have emerged in the Central/Plains, Mid-Atlantic, and New England States.

The study findings confirm three realities of forest regeneration management for forests under herbivory stress in the Midwest and Northeast: 1) The scope and persistence of large-ungulate herbivory has long-term wide-ranging implications for regeneration management; 2) less palatable tree species will continue to have a competitive advantage during the regeneration phase and are likely to be different species from the current canopy dominants; and 3) successful regeneration management of these forests requires more emphasis on ungulate-compatible prescriptions, novel approaches, and adaptive science.

**Cover Photo:** White-tailed deer herd. Photo by Garen Meguerian, via Flickr.com, used with permission.

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**William H. McWilliams, James A. Westfall, Patrick H. Brose, Daniel C. Dey, Anthony W. D'Amato, Yvette L. Dickinson, Mary Ann Fajvan, Laura S. Kenefic, Christel C. Kern, Kenneth M. Laustsen, Shawn L. Lehman, Randall S. Morin, Todd E. Ristau, Alejandro A. Royo, Andrew M. Stoltman, and Susan L. Stout**

## ABOUT THE AUTHORS

**William H. McWilliams** is a research forester with the Forest Inventory and Analysis program at the Northern Research Station, USDA Forest Service, Newtown Square, PA.

**James A. Westfall** is a research forester with the Forest Inventory and Analysis program at the Northern Research Station, USDA Forest Service, Newtown Square, PA.

**Patrick H. Brose** is a research forester with the Sustaining Forests in a Changing Environment project at the Northern Research Station, USDA Forest Service, Irvine, PA.

**Daniel C. Dey** is project leader of the Sustainable Management of Central Hardwood Ecosystems and Landscapes project at the Northern Research Station, USDA Forest Service, Columbia, MO.

**Anthony W. D'Amato** is a professor at the Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT.

**Yvette L. Dickinson** is an assistant professor at the School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI.

**Mary Ann Fajvan** is a research forester with the Ecology and Management of Invasive Species and Forest Ecosystems program at the Northern Research Station, USDA Forest Service, Morgantown, WV.

**Laura S. Kenefic** is a research forester with the Center for Research on Ecological Change at the Northern Research Station, USDA Forest Service, Bradley, ME.

**Christel C. Kern** is a research forester with the Center for Research on Ecological Change at the Northern Research Station, USDA Forest Service, Bradley, ME.

**Kenneth M. Laustsen** is a forest biometrician with the Maine Forest Service, Augusta, ME.

**Shawn L. Lehman** is section chief, Inventory & Monitoring Section for the Bureau of Forestry, Pennsylvania Department of Conservation and Natural Resources, Harrisburg, PA.

**Randall S. Morin** is a research forester with the Forest Inventory and Analysis program at the Northern Research Station, USDA Forest Service, Newtown Square, PA.

**Todd E. Ristau** is a research forester with the Sustaining Forests in a Changing Environment project at the Northern Research Station, USDA Forest Service, Irvine, PA.

**Alejandro A. Royo** is a research forester with the Sustaining Forests in a Changing Environment project at the Northern Research Station, USDA Forest Service, Irvine, PA.

**Andrew M. Stoltman** is a rural and urban forest inventory analyst with the Wisconsin Division of Forestry, Madison, WI.

**Susan L. Stout** is project leader with the Sustaining Forests in a Changing Environment project at the Northern Research Station, USDA Forest Service, Irvine, PA.

### ENGLISH EQUIVALENTS

| When you know metric: | Multiply by conversion factor | To convert to English: |
|---|---|---|
| Kilometers | 0.621 | Miles |
| Meters | 3.281 | Feet |
| Hectares | 2.471 | Acres |

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## ACKNOWLEDGMENTS

The authors would like to thank all of the field staff members who conducted the browse impact evaluations across such a wide range of conditions. The evaluations are completed along with measurements of other ecological indicator variables, making for an arduous and challenging field season. Without the hard work of these experts, the difficult job of evaluating browse impact could not have been completed within quality assurance tolerances. We are also grateful to those who provided valuable feedback on an earlier version of this document: Mark Nelson, Forest Service; Henry McNab, Forest Service; and three anonymous peers. All their comments were incorporated and the improvements are very apparent to the authors.

# INTRODUCTION

In the forests of the 24-State midwestern and northeastern United States, herbivory (hereafter, "browse") by large ungulates directly influences ecological function, values, and services over the lifespan of forest stands by setting compositional and structural trajectories during the stand-initiation phase of forest development (Côté et al. 2004, Hobbs et al. 2013, Waller and Alverson 1997). Historically, white-tailed deer (*Odocoileus virginianus*) have been at the center of research to understand and forestall large-ungulate impacts on forest regeneration in the Midwest and Northeast. Deer browse was recognized as an important factor affecting understory plant communities in the region as early as 1915 (Frothingham 1915). Over the past decade or so, the role of moose (*Alces alces*) has become an issue in forest regeneration (Wattles and DeStefano 2011).

Browse alters growth rates, successional pathways, plant architecture, nutrient and litter cycling, and soil microenvironments (Witt and Webster 2010). Browse reduces the number of understory taxa by removing edible native plants, thereby increasing biotic homogenization of the forest understory (Augustine and McNaughton 1998, McKinney and Lockwood 1999, Olden et al. 2004, Rooney et al. 2004). In the overstory, oaks (*Quercus* spp.), red and sugar maple (*Acer rubrum* and *A. saccharum*), hickories (*Carya* spp.), northern white-cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), and aspen (*Populus tremuloides* and *P. grandidentata*) have been reported as having difficulty sustaining presence and abundance due to high browse, which limits regeneration and recruitment into the overstory in portions of their range (Dey 2014, McWilliams et al. 1995, Rooney and Waller 2003, White 2012). Large-ungulate browse also influences floral diversity and food webs (biomass, and seed and mast production) by modifying the quality and productivity of faunal habitat at multiple trophic levels, as indicated by insect and bird density (Bressette et al. 2012, Horsley et al. 2003, Nuttle et al. 2011).

Large-ungulate browse is an agent of change that combines with other controlling factors to alter forest regeneration potential in the Midwest and Northeast.

White-tailed deer herd. Photo by USDA Forest Service.

Key ecological factors with negative consequences for forest regeneration are mesophication (Nowacki and Abrams 2008), wildfire exclusion (Abrams 1992, Brose 2014), soil nutrient degradation (Bailey et. al. 2005, Driscoll et al. 2001, Kardol et al. 2014), and forest land conversion (Drummond and Loveland 2010, Nowacki and Abrams 2014). Other controlling factors are forest fragmentation (Allen et al. 2013), native and alien plant invasion (Knight et al. 2009, Royo and Carson 2006), native and alien pests and diseases (Lovett et al. 2016, Potter and Conkling 2016), and climate change (Dukes et al. 2009, Iverson et al. 2008). Gaps in knowledge about multifactor interactions heighten the need for novel forest management approaches based on local conditions.

Seventy years ago, Aldo Leopold and others (1947) made projections about which areas in the continental United States would be susceptible to overbrowsing of nutritive plants because of deer overpopulation. He and his colleagues mapped areas of deer presence and absence, and identified areas of expected deer overpopulation, where browse pressure would leave plants that have little or no nutritive value. Recent measurements of browse impacts on forest inventory plots in the Midwest and Northeast provide the opportunity to review this pioneering work.

The goals of this report are twofold. The first goal is to review existing historical mapping efforts in light of the new findings on browse impacts presented here. Beguin et al. (2016) have developed a holistic, hierarchical framework of guidelines and information gaps for ungulate-forest systems globally. This report focuses on the extent and severity of browse impacts for the Midwest and Northeast. The second goal is to present a synoptic review of expected implications for regeneration management to restore forests under browse stress based on the assumption that forests with at least moderate impacts require consideration of ameliorative management prescriptions. Specific objectives are to review maps of deer presence and density, evaluate the extent of browse, identify browse problem areas and forest-type groups under pressure, and summarize implications for forest regeneration management. The results are a visual depiction of the role of browse in forest regeneration management that indicates where managers will most likely need to consider these implications in forest and habitat restoration efforts to overcome severe and perennial difficulties.

## MAPPING DEER DENSITY

In the past, State wildlife agencies have collected and maintained geographic information on deer browse impacts. Most mapping efforts have used deer density expressed as the number of deer per square mile of forest land. Such maps typically use deer density estimates from different models, hunting results, deer-vehicle collision reports, and opinion surveys. Application of deer density information assumes that thresholds for delineating problem areas are known. For example, Tilghman (1989) found that it is necessary to keep densities at less than 18 deer per acre to allow development of healthy forest understory in northwestern Pennsylvania. The diversity of forest ecosystems, disparate modeling approaches, and lack of biome-specific thresholds limit the usefulness of deer density for large-scale maps covering multiple States. Maps covering the eastern United States are described next as an introduction to a new visualization based on empirical data collected consistently across the Midwest and Northeast.

### Mapping Efforts in 1947

Leopold and his colleagues published a foundational survey in 1947 to assess deer populations and condition of their range across the United States (Fig. 1). The objective was to delineate areas where high-density deer populations would lead to reductions of carrying capacity, causing an imbalance between herd size and available food. The concern was that overbrowsed nutritive plants would be replaced by plants with little to no nutritive value (Leopold et al. 1943). Though this work was innovative at the time, it was largely based on the personal experience of observers, which precludes statistical comparison with the new visualization presented here.

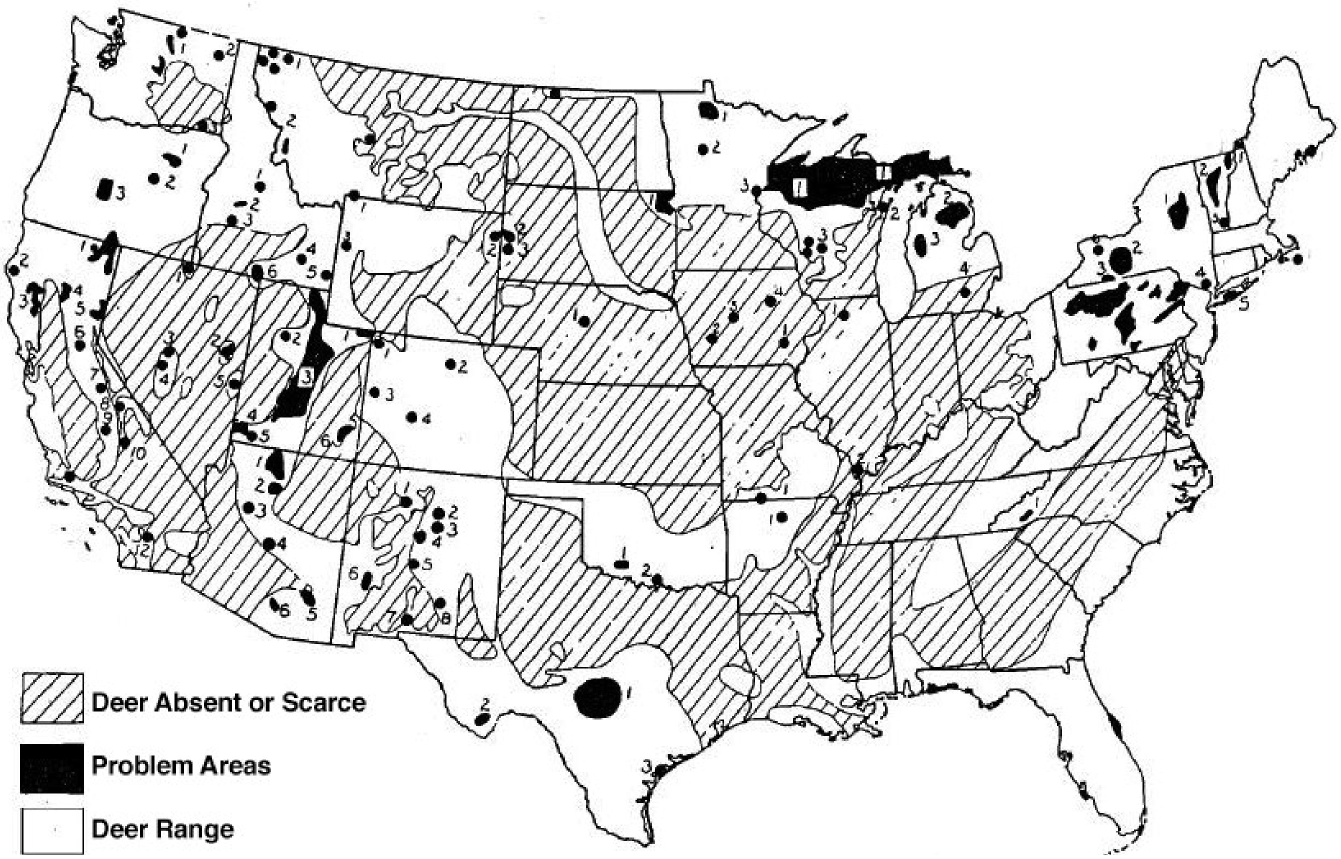


Figure 1.—Areas in which overpopulations of deer now exist or have existed in the recent past (as of 1947), contiguous United States (Leopold et al. 1947). Numbers refer to case histories. Map used with permission of Wiley Inc., with copyright retained by The Wildlife Society.

## Mapping Efforts in 1950, 1970, 1980, 1982, and 1988

In the 1980s, population occurrence and density maps were developed as part of a series of investigations into the geographic distribution of cloven-hoofed animals susceptible to hand-foot-and-mouth disease (*Coxsackie* viral infection) for the continental United States. The project assisted efforts by the University of Georgia (n.d.) to stem prospective outbreaks in humans. The project created county-level thematic maps for the southern United States for 1950, 1970, and 1980 (Fig. 2), and for the eastern United States for 1982 and 1988 (Fig. 3). Trends cannot be determined reliably for a variety of reasons. Details of the specific methodologies used may differ from year to year because descriptions of earlier survey methods were not always available and agencies often used different population models from survey to survey. Estimation techniques were also improved over time. Although the study ended in 1988 (John Fischer, University of Georgia, College of Veterinary Medicine, pers. comm., 2017), these visualizations offer monumental insight into how deer browse levels and associated impacts have changed across the Midwest, Northeast, and beyond since Leopold and his colleagues made their original map.

The visualization for 1950 shows deer population occurrences in the southern United States that appear new since Leopold and others' work though early data limitations explain some of the expansion depicted. Specifically, Leopold and colleagues did not obtain data from the mountains of West Virginia and Virginia; the Piedmont of Virginia; the Atlantic coast of Georgia, North Carolina, and South Carolina; and riverine systems in Alabama, Georgia, and Mississippi. The results for 1970 and 1980 reveal a much larger estimate of density across the South. The findings for 1982 and 1988 indicate that extensive well-established populations throughout the eastern United States exceed the "environmental capacity," defined as 15 deer per square mile of forest.

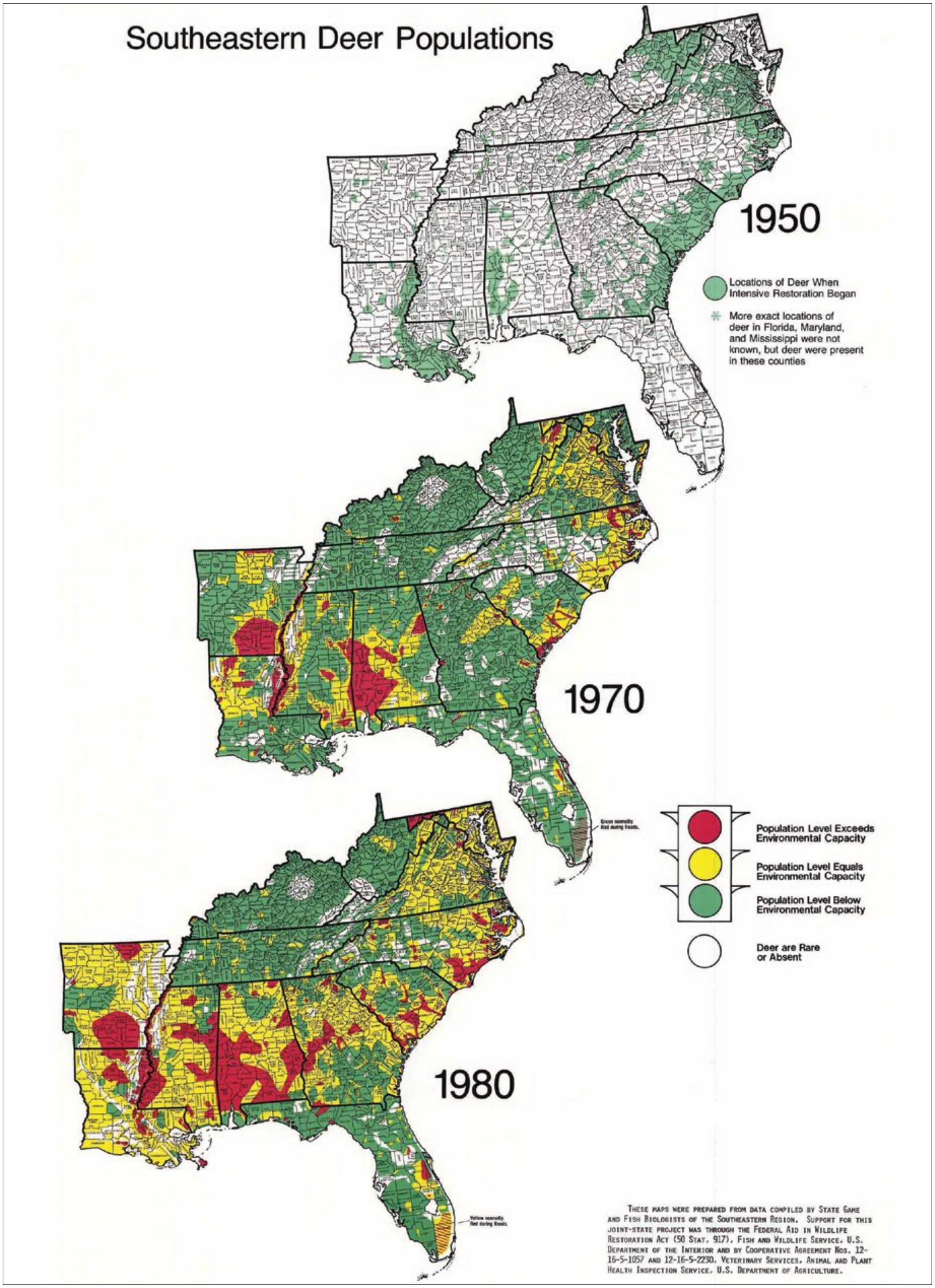


Figure 2.—White-tailed deer population density, southern United States, 1950, 1970, and 1980 (Southeastern Cooperative Wildlife Disease Study [University of Georgia, n.d.], used with permission).

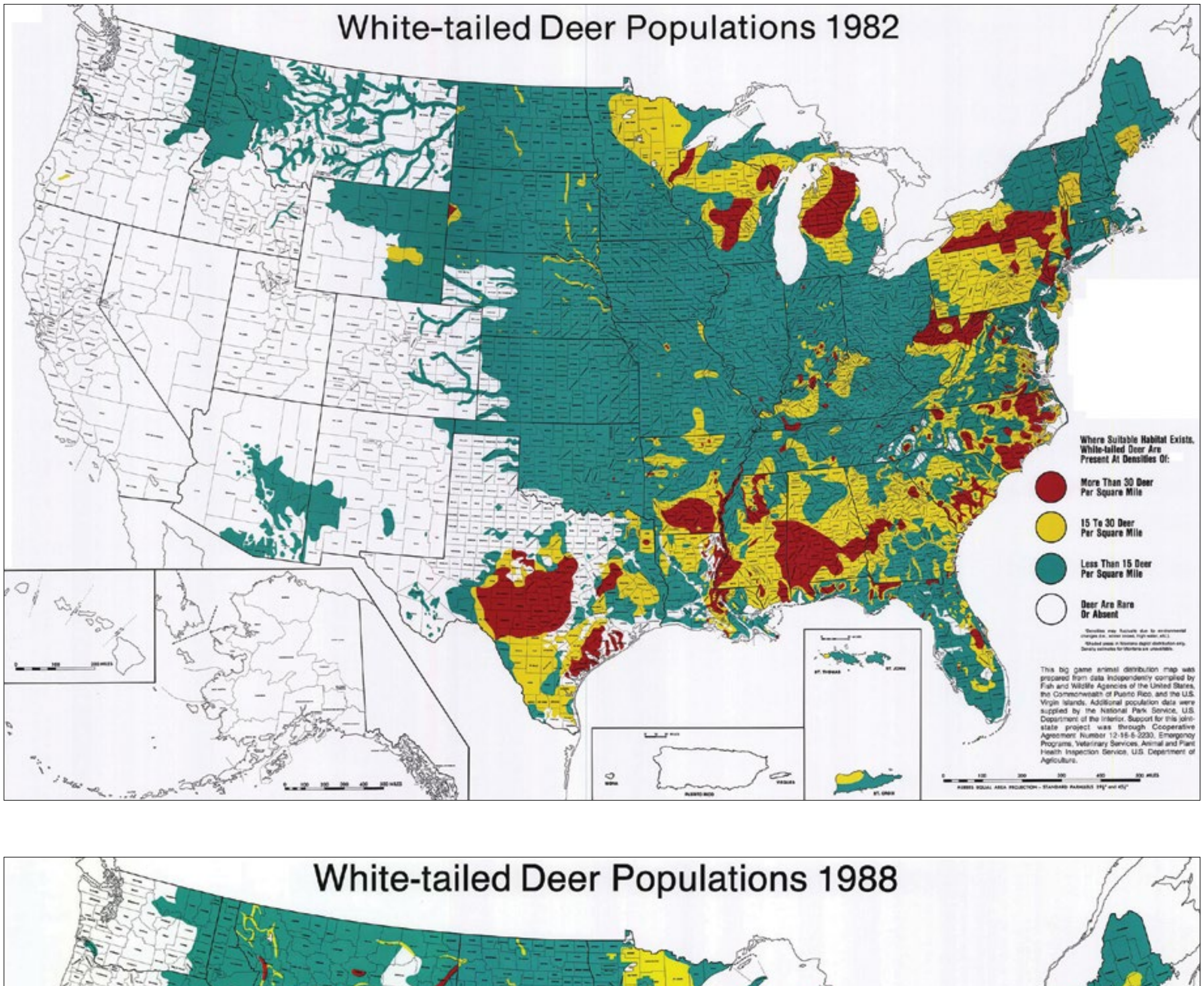


Figure 3.—White-tailed deer population density, eastern United States, 1982 and 1988 (Southeastern Cooperative Wildlife Disease Study [University of Georgia, n.d.], used with permission).

American beech (*Fagus grandifolia*). Photo by William H. McWilliams, USDA Forest Service.

## Mapping Efforts from 2001 through 2005

A more recent county thematic map was published for the eastern United States for 2001 through 2005 (Russell et al. 2017, Walters et al. 2016) (Fig. 4). The map was produced by the Quality Deer Management Association (QDMA) as an informative aid for deer hunters. The limitations of the map are that it is based on information by State agencies that use different population estimation procedures and that these methods are not repeatable because some agencies now use improved approaches or no longer attempt to estimate population levels (Kip Adams, Director of Education and Outreach, QDMA, pers. comm., 2014). Despite these caveats, the map clearly depicts deer density information for this region ca. 2005.

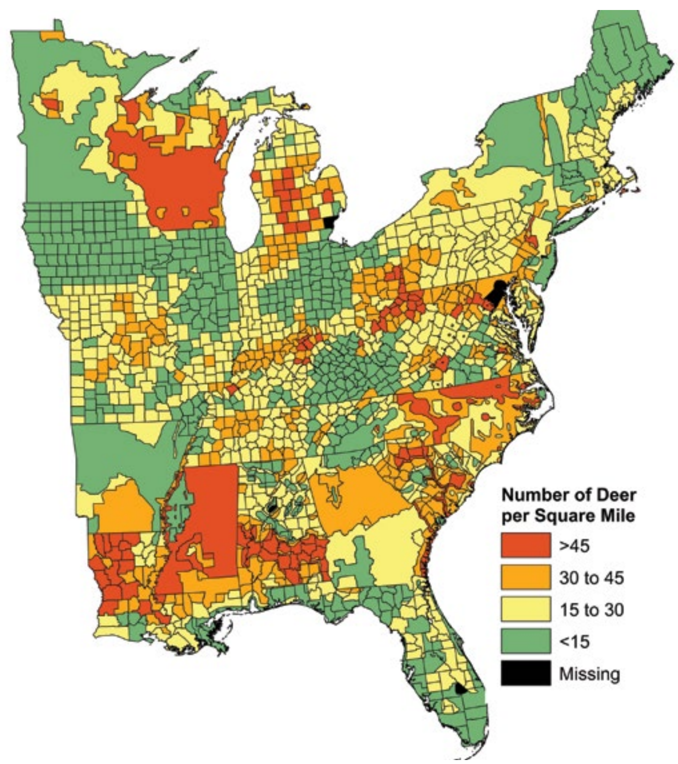


Figure 4.—White-tailed deer density per square mile of land area, eastern United States, ca. 2005 (Walters et al. 2016).

# METHODS

## STUDY REGION

The Midwest (Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, North Dakota, Ohio, South Dakota, and Wisconsin) and Northeast (Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, and West Virginia) contain 182.4 million acres of forest land covering 29 percent of the land surface of the study region (Miles 2018). Forest land is an integral provider of ecological services, such as clean water, clear air, biodiversity, wildlife habitat, and carbon storage; and economic benefits, such as housing, infrastructure, fine-wood products, and paper. The following statistics illustrate the importance of the region: It is home to half of the American population, represents more than one-third of the forest carbon stored, and accounts for just over half of the hardwood roundwood production of the continental United States (Oswalt et al. 2014).

Located between 35 and 50° N latitude and 66 and 105° W longitude, the region ranges in elevation from sea level to more than 6,900 feet. Climate varies widely across the region, with average annual temperature ranging from 32 to 61 °F, increasing from north to south. Average precipitation varies from 10 to 50 inches per year, increasing from west to east. The region's forests occur in portions of the Prairie, Warm Continental, Hot Continental, and Subtropical ecological divisions, and encompass all or part of 16 ecological provinces (Cleland et al. 2007). For this study, provinces were grouped into four ecological subdivisions: Central/Plains, Lake, Mid-Atlantic, and New England. The delineations do not follow State boundaries, but were based on broad ecological, physiographic, and phenologic characteristics to facilitate discussion of regeneration management issues for the major forest-type groups under browse pressure (Figs. 5 and 6, Table 1).

American woodcock (*Scolopax minor*). Photo by Ricky Layson Photography, via bugwood.com, used with permission.

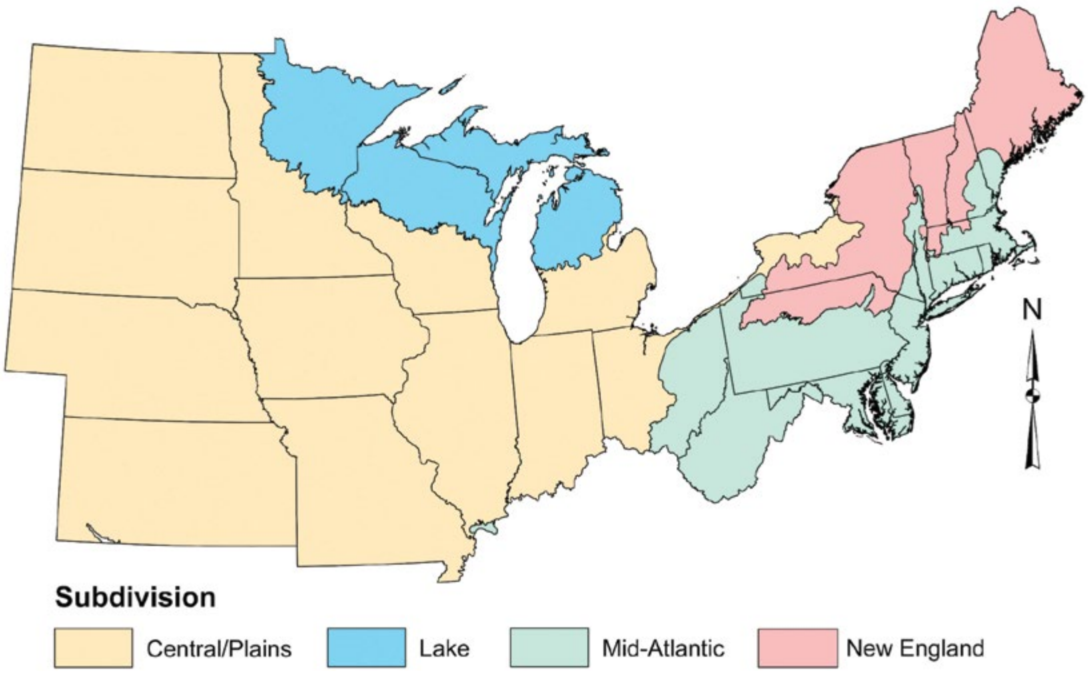

Figure 5.—Location of ecological subdivisions used for analysis (Cleland et al. 2007), Midwest and Northeast.

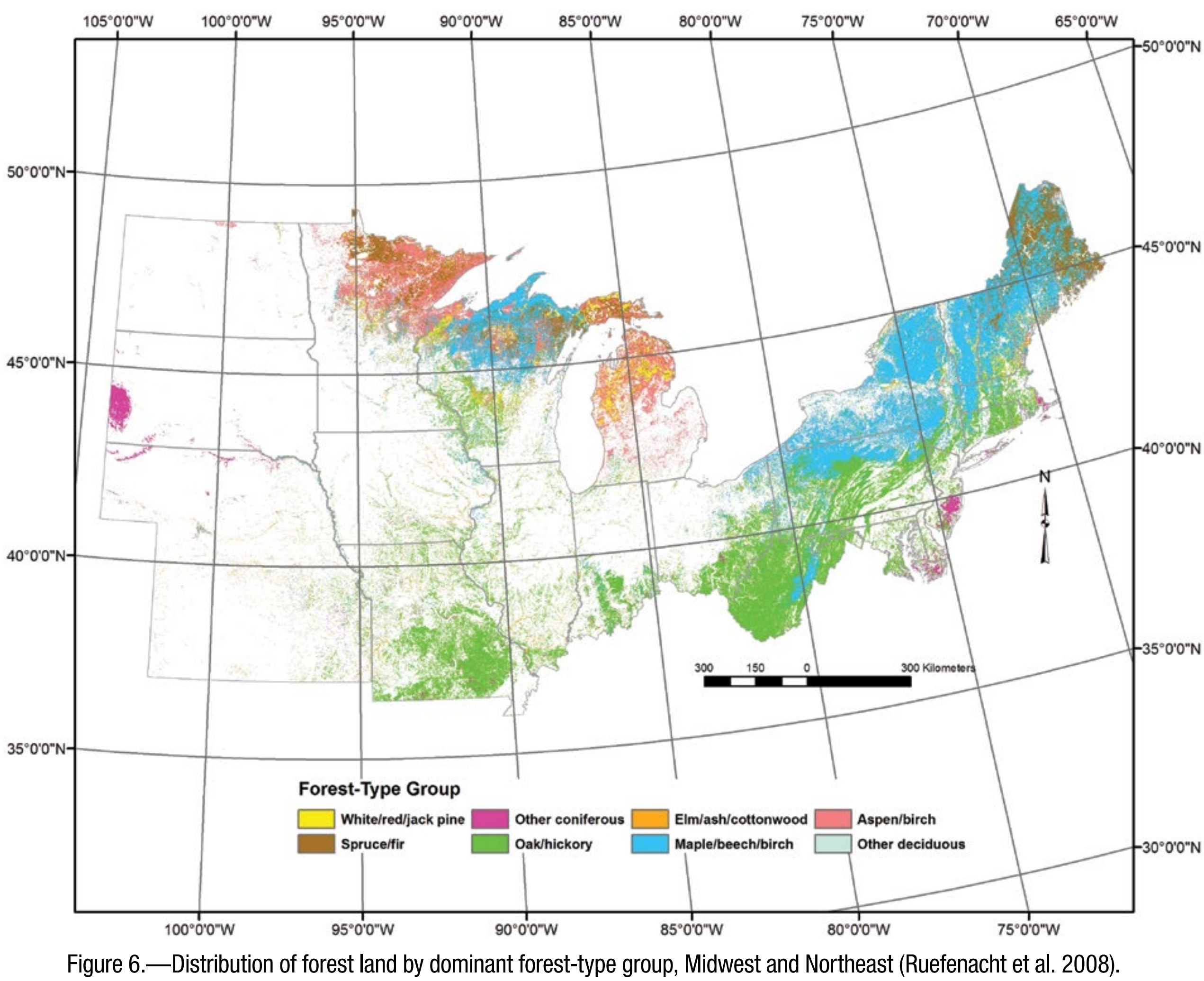

Figure 6.—Distribution of forest land by dominant forest-type group, Midwest and Northeast (Ruefenacht et al. 2008).

Table 1.—Percentage of forest land area and total aboveground biomass for the five most prevalent forest-type groups and taxa, by ecological subdivision, Midwest and Northeast, 2017.

| Forest-type group | Percentage of forest land | Taxa | Percentage of aboveground biomass |
|---|---|---|---|
| **All subdivisions** | | | |
| Oak/hickory | 36 | Maple | 23 |
| Maple/beech/birch | 25 | Red oak | 13 |
| Aspen/birch | 9 | White oak | 10 |
| Spruce/fir | 8 | Ash | 5 |
| Elm/ash/cottonwood | 8 | Hickory/walnut | 5 |
| Other | 14 | Other | 44 |
| **Total acres** | **182,359,696** | **Total short tons** | **9,135,017,184** |
| **Central/Plains** | | | |
| Oak/hickory | 60 | White oak | 19 |
| Elm/ash/cottonwood | 16 | Red oak | 17 |
| Maple/beech/birch | 6 | Maple | 13 |
| Oak/pine | 4 | Hickory/walnut | 11 |
| Ponderosa pine | 3 | Ash | 6 |
| Other | 11 | Other | 34 |
| **Total acres** | **50,666,979** | **Total short tons** | **2,267,355,719** |
| **Lake** | | | |
| Aspen/birch | 26 | Maple | 28 |
| Maple/beech/birch | 23 | Red oak | 14 |
| Spruce/fir | 19 | Eastern white/red pine | 9 |
| Oak/hickory | 10 | Red oak | 8 |
| White/red/jack pine | 9 | Spruce/fir | 8 |
| Other | 13 | Other | 33 |
| **Total acres** | **42,822,294** | **Total short tons** | **1,521,565,869** |
| **Mid-Atlantic** | | | |
| Oak/hickory | 61 | Maple | 20 |
| Maple/beech/birch | 18 | Cottonwood/aspen | 18 |
| Elm/ash/cottonwood | 5 | White oak | 14 |
| Oak/pine | 5 | Yellow-poplar | 7 |
| Other coniferous | 3 | Hickory/walnut | 6 |
| Other | 8 | Other | 35 |
| **Total acres** | **42,800,614** | **Total short tons** | **2,839,611,768** |
| **New England** | | | |
| Maple/beech/birch | 54 | Maple | 32 |
| Spruce/fir | 16 | Spruce/fir | 10 |
| Oak/hickory | 10 | Red oak | 7 |
| White/red/jack pine | 7 | Yellow birch | 7 |
| Aspen/birch | 6 | Beech | 6 |
| Other | 7 | Other | 38 |
| **Total acres** | **44,833,504** | **Total short tons** | **2,455,026,692** |

The study region has 96 percent of the Nation's maple/beech/birch (*Acer/Fagus/Betula*) and 42 percent of the oak/hickory (*Quercus/Carya*) forest land, and species associated with these groups have comparable amounts of total aboveground biomas. These forest-type groups make up 25 percent and 36 percent, respectively, of the total forest land in the region. Aspen/birch (*Populus/Betula*) (9 percent), spruce/fir (*Picea/Abies*) (8 percent), elm/ash/cottonwood (*Ulmus/Fraxinus/Populus*) (8 percent), white/red/jack pine (*P. strobus/P. resinosa/P. banksiana*) (5 percent), and other miscellaneous coniferous and deciduous forests make up the rest (Miles 2018).

## FOREST MONITORING IN THE MIDWEST AND NORTHEAST

Monitoring results for large-ungulate effects on forest regeneration were obtained using new measurement protocols covering regeneration and browse as part of the three-phase regionwide forest inventory conducted by the USDA Forest Service, Northern Research Station, Forest Inventory and Analysis (NRS-FIA) program (Bechtold and Patterson 2005). Phase 1 uses classified remote sensing imagery to stratify sample plots and reduce uncertainty (variance) for estimates of population totals (McRoberts et al. 2006).

In Phase 2, sample plots are visited and field measurements taken on forested conditions throughout the year at an intensity of one plot per roughly 5,500 acres. Each sample plot is made up of a cluster of four 24-foot fixed-radius subplots. Each subplot contains a 6.8-foot-radius microplot offset from the subplot center (USDA Forest Service 2016).

In Phase 3, data for a suite of enhanced ecological indicators are collected on a subset of NRS-FIA Phase 2 plots sampled during the leaf-on summer season at an intensity of one plot per 95,998 acres (USDA Forest Service 2017). A regeneration indicator (RI) was added as a Phase 3 indicator starting in 2012 (McWilliams et al. 2015). (The subset of Phase 2 plots is sometimes referred to as "Phase 2-plus.") This study used 4,162 Phase 3 RI sample plots completed from 2012 to 2017 (Table 2). All of the data used in this study are publicly available from the NRS-FIA data portal (https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html).

The RI protocols include browse-impact severity evaluation and seedling measurements not included on Phase 2 plots. That is, all established seedlings from 2.5 inches in height and less than 5.0 inches in diameter at breast height (minimum diameter for saplings) are counted by seedling height class (2.0 to 5.9 inches, 6.0 to 11.9 inches, 1.0 to 2.9 feet, 3.0 to 4.9 feet, 5.0 to 9.9 feet, and 10 feet and higher). The browse-impact severity evaluation indicates the amount of stress that herbivores are exerting on tree seedlings and other understory flora.

As used here, browse is defined as animals' consumption of tender shoots, twigs, and leaves of trees or shrubs for food (USDA Forest Service 2017). The browse evaluation does not target specific edible taxa because forests under browse stress may lack palatable vegetation. Latham et al. (2005) summarize the difficulty of evaluating browse in heavily used regions by noting that it depends on what is available, which further depends on local population density, recent trends in density, alternative food sources, adjacent land uses, disturbance history, snow cover, and other factors. This means that even though food preference lists are available (see Atwood [1941]), herbivores' preferences are known to differ by season and region for the same forest type (Latham et al. 2005, Stiteler and Shaw 1966). The coding system was developed for forest ecosystems under browse pressure from white-tailed deer in the Northeast (Brose et al. 2008, Marquis et al. 1992). Guidelines for assessing impacts of moose and other browsers, such as elk (*Cervus canadensis*), or snowshoe hare (*Lepus americanus*), are not available in the literature, but their impacts were evaluated if they met the following deer browse-impact definitions:

**Low:** Plot is inside a well-maintained fence or minimal browsing is observed, or vigorous seedlings are present and of varied height if no well-maintained fence is present. Herbaceous plants are present and are able to complete their life cycles.

**Moderate:** Evidence of browsing is observed but not common. Seedlings are common but with limited variability in height. Stump sprouts are heavily browsed or not present. Herbaceous plants show a lack of or inhibited flowering and fruiting. There is little or no evidence of browsing on nonpreferred plants.

**Table 2.—Number of sample locations on forest land, by ecological subdivision and province (Cleland et al. 2007), Midwest and Northeast.**

| Subdivision | Number of samples |
|---|---|
| **Central/Plains** | |
| Central Interior Broadleaf Forest (223) | 403 |
| Lower Mississippi Riverine Forest (234) | 1 |
| Midwest Broadleaf Forest (222) | 403 |
| Prairie Parkland (Temperate) (251) | 256 |
| Prairie Parkland (Subtropical) (255) | 7 |
| Southeastern Mixed Forest (231) | 4 |
| Great Plains-Palouse Dry Step (331) | 24 |
| Great Plains Steppe (332) | 66 |
| Black Hills Coniferous Forest (M334) | 22 |
| Southwest Plateau and Plains Dry Steppe and Shrub (315) | 1 |
| **Subtotal** | **1,187** |
| **Lake** | |
| Laurentian Mixed Forest (212) | **897** |
| **Mid-Atlantic** | |
| Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow (M221) | 354 |
| Eastern Broadleaf Forest (221) | 582 |
| Outer Coastal Plain Mixed Forest (232) | 70 |
| **Subtotal** | **1,006** |
| **New England** | |
| Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow (M211) | 447 |
| Northeastern Mixed Forest (211) | 625 |
| **Subtotal** | **1,072** |
| **All** | **4,162** |

**High:** Evidence of browsing is common on preferred vegetation. Preferred seedlings and herbaceous plants are rare or absent. Nonpreferred plants show some evidence of browsing. Browse-resistant vegetation is limited in height growth. Evidence of browsing is everywhere. Nonpreferred, browse-resistant plants show signs of heavy repeated browsing, and a browse line is present.

Field crews evaluate browse impact for the forest land portion of the four subplots. The evaluation can be challenging due to variability in understory communities, variability in site quality, and other factors. For example, though the coding system was designed with the flexibility to cover a wide range of forest types across a very large geographic area, there is some variability among types that is not fully accounted for during the assessment. The aspen type within the aspen/birch forest-type group is a good example because it regenerates primarily by coppice. A collective 90 percent of the aspen forest type in the study region is in Minnesota (40 percent), Michigan (19 percent), Maine (19 percent), and Wisconsin (12 percent); aspen in these States is considered a medium-quality food that is consumed after preferred taxa such as maple, white pine, and northern white-cedar (Michigan State University Cooperative Extension Service 1967). Aspen is recognized for prolific root sprouting that has been estimated as 10 times the amount produced by associated conifers, and young "sucker" stands can withstand consumption of up to 50 percent and still be considered to have an acceptable number of stems (Sampson 1919). This means that analysis of results for aspen may show lower probabilities of occurrence, as is evident in northern Minnesota.

Ungulate population density and factors outside the evaluation area (e.g., alternative food sources) further complicate the assessment. To overcome these issues, field staff members are trained by expert crews, certified by trainers, and subject to annual quality assurance checks. Another favorable element is that the field crews visit plots on an interpenetrating annualized sample grid. This sampling approach means that they visit the entire work region each year and are familiar with local forest conditions.

Note that NRS-FIA does not take measurements in some urbanized areas and nonforest conditions where very high browse pressure is common. Forest conditions where ungulates are typically concentrated, but where few FIA samples are collected, are fragmented forests consisting of smaller tracts and strips, and riparian forests.

## VISUALIZING BROWSE IMPACTS

New empirical-based monitoring results for large-ungulate browse impacts presented here provide an opportunity to assess this issue in a spatial context. The underlying assumption is that the severity of these impacts indicates where adaptive or corrective management will most likely be needed for redirecting forest succession after a stand-initiating disturbance.

The browse-impact code was used to generate a geospatial visualization for the Midwest and Northeast. Geographic analysis is challenging because of diverse physiography, diverse soils, and fluctuating seasonal and annual ungulate populations, as well as the wide range of floral and faunal phenologies among taxa that are endemic to the study region. Indicator kriging offers a means of addressing these issues. The indicator kriging function in Esri's ArcMap 10.2.2 Geostatistical Analyst package was used to create interpolated surfaces from sample location coordinates (Isaaks and Srivastava 1989). Predictions using indicator kriging are presented as the probability of occurrence for moderate or high browse impacts. It was not feasible to produce a separate visualization for high impacts because of the limited number of samples relative to the large region modeled. Indicator kriging models use autocorrelation between observations as a function of distance assuming the following model:

$$I(s) = \mu + \varepsilon(s),$$

where $\mu$ is an unknown constant, $\varepsilon(s)$ is the random autocorrelation error, and $I(s)$ is a binary variable. The two browse-code classes were combined and converted to binary data, and the modeled semivariogram parameters (nugget and partial sill) were optimized by using cross-validation with a focus on estimating the range parameter. The semivariogram optimization was based on minimizing the mean squared error (see the semivariogram and model parameters in Figure 7A). Indicator kriging was then used to predict the probability of the moderate and high browse-impact classes. In the cross-validation of observed versus predicted values (Fig. 7B), the range and medians of the predicted probabilities increase with the observed browse classes as expected. A nonforest mask was then applied to display modeled browse impact only on forested areas based on the work of Wilson et al. (2012). The final spatial product depicts the probability of a binary value that represents moderate or high ungulate browse impacts occurring at a given pixel. A kriged surface of the distribution of standard errors for the probability of occurrence estimates was created to portray spatial variation across the study region (Fig. 8).

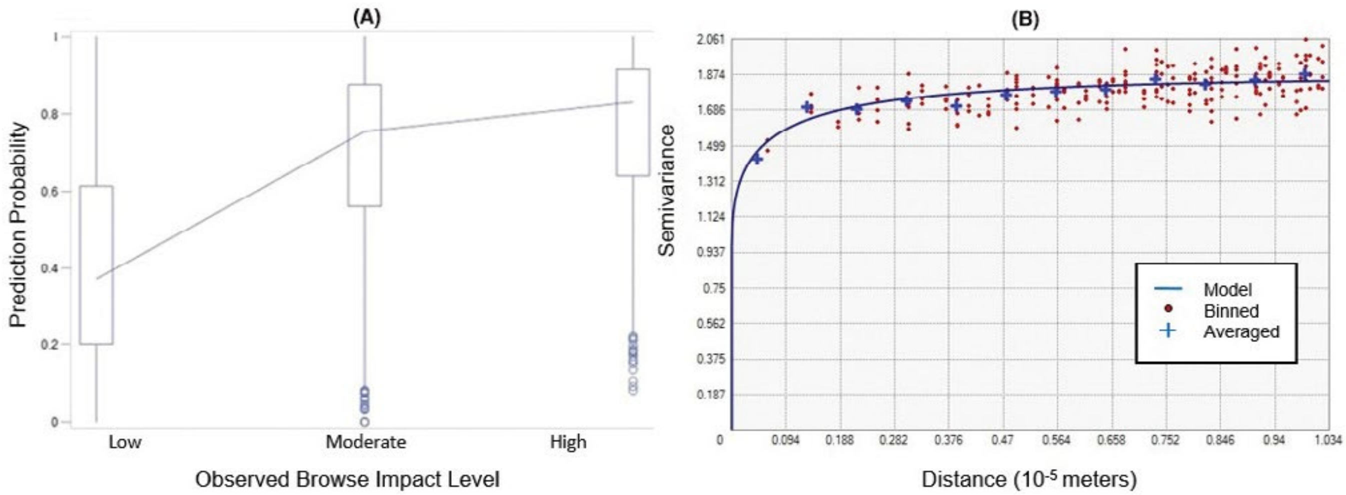


Figure 7.—Predicted probabilities by browse impact code (A). The lower and upper edges of the boxes represent the 25th and 75th percentiles and the line connects the median values (50th percentile). Vertical lines are the extreme points for the 1.5 interquartile ranges, and values outside this range are represented by circles. Semivariogram for the indicator kriging model where output pixel size is 10 km, lag size is 8.6 km, number of lags is 12, range is 68.9 km, nugget is 0.0977, and sill is 0.0889 (B).

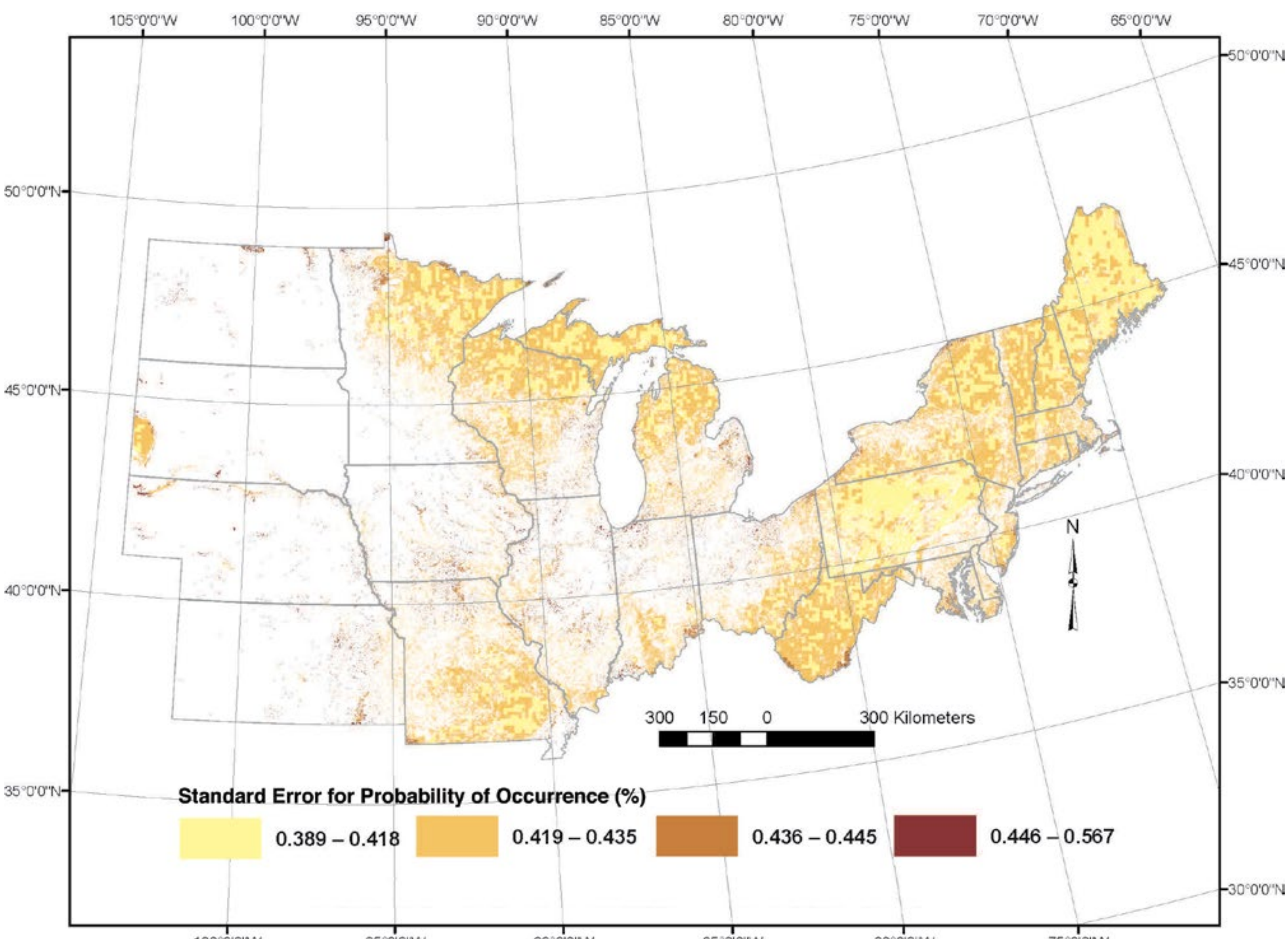


Figure 8.—Distribution of standard errors of estimates of probability of occurrence for browse impact visualization (Fig. 9), Midwest and Northeast, 2017.

# RESULTS

The visualization of browse impacts depicts broad regions where forest managers and others tasked with reforestation should consider browse impacts when planning for regeneration (Fig. 9). A probability of more than 70 percent is a somewhat arbitrary but useful and well-described minimum for identifying areas where forest managers need to consider local browse pressure (Brose et al. 2008, Rosenberry et al. 2009). This range is based broadly on the percentage of silvicultural samples required to prescribe certain management actions based on regeneration survey samples (Marquis et al. 1992). Areas with probabilities greater than 70 percent for moderate or high impacts were found in the northern highlands of Wisconsin; the western Upper Peninsula and northern Lower Peninsula of Michigan; the Ozark Highlands of southwestern Missouri; the southern portions of Illinois, Indiana, and Ohio; the Appalachian Mountains, which cover much of the Mid-Atlantic States, New York, and southern New England; New Hampshire; and Vermont.

Probabilities from 31 percent to 70 percent provide a practical range for identifying areas where consideration of local browse conditions is advisable. Areas in this range are scattered throughout the eastern Mid-Atlantic States; and the southern Adirondack Mountains, Mohawk River Valley, and Appalachian Plateau of New

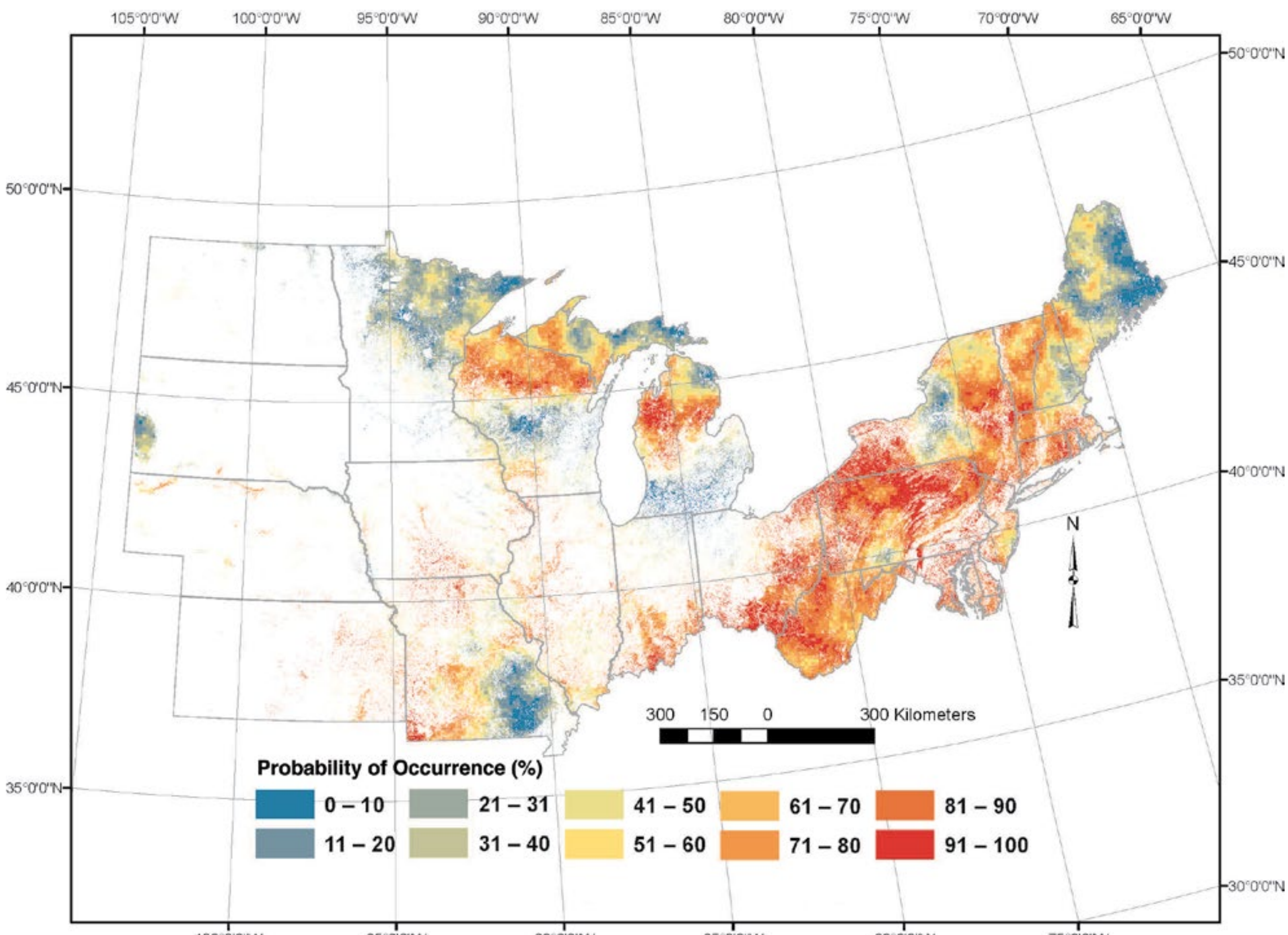


Figure 9.—Probability of occurrence for moderate or high ungulate browse impacts on forest land, Midwest and Northeast, 2017.

York. Areas with probabilities of 30 percent or less probably do not warrant measures to control ungulate pressure in management prescriptions. These areas are most common in the Ozark Highlands of southeastern Missouri, and the Aroostook uplands and eastern interior of Maine.

Review of Leopold and others' 1947 map of overpopulated deer ranges in the context of the visualization of browse effects presented here offers insight into the longevity of existing problem areas and new areas of browse stress that have emerged over the past 70 years. Leopold and others' deer survey identified seven major problem areas in the Midwest and Northeast: northern Wisconsin, the Upper Peninsula and northern Lower Peninsula of Michigan, most of Pennsylvania, the Adirondack region of New York, southwestern New York, and Vermont. The 1947 map showed that deer were absent or scarce in the rest of the region. The findings presented here show that the problem areas Leopold and others described have persisted, and areas of concern have expanded to Illinois, Indiana, Ohio, West Virginia, Maryland, Delaware, New Jersey, and the southern New England States. The review did not indicate any areas where deer problem areas were reduced.

As a general guideline, management prescriptions to minimize species loss and encourage regeneration of desirable tree species should be considered in areas when impacts are moderate or high and where tree reproduction is absent or healthy seedling development is not possible without additional management inputs (Brose et al. 2008). The original Phase 3 RI samples used to generate the visualization provide estimates of the percentage of forest land with moderate or high browse impacts for subdivisions and forest-type groups. Overall, 59 percent of the forest land in the Midwest and Northeast had evidence of moderate or high impacts (Fig. 10). The Mid-Atlantic subdivision had the highest proportion (79 percent) of forest land with moderate or high impacts, followed by the Central/Plains (61 percent). The levels of moderate or high impacts were below the regional average for the Lake (43 percent) and New England (45 percent) subdivisions.

The oak/hickory and maple/beech/birch forest-type groups had the highest percentage of forest land with moderate or high browse impacts, 69 percent and 65 percent, respectively (Fig. 11). Elm/ash/cottonwood and other deciduous forest-type groups had percentages near the regional average. For spruce/fir, aspen/birch, white/red/jack pine, and other coniferous forest-type groups, the proportion was less than the regional average.

Pine Creek Gorge, Pennsylvania. Photo by William H. McWilliams, USDA Forest Service.

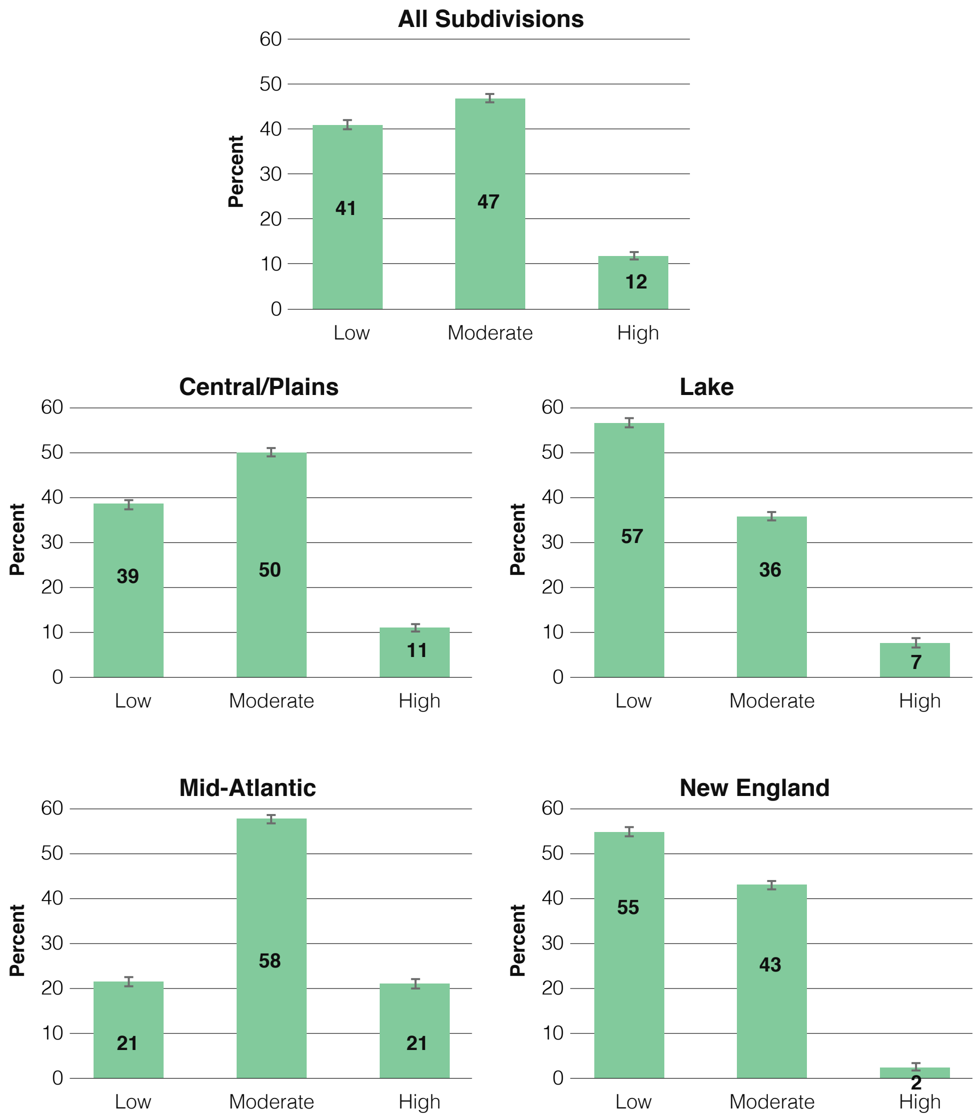


Figure 10.—Percentage of forest land by ecological subdivision and browse impact code, Midwest and Northeast, 2017. Error bars represent 68 percent confidence intervals.

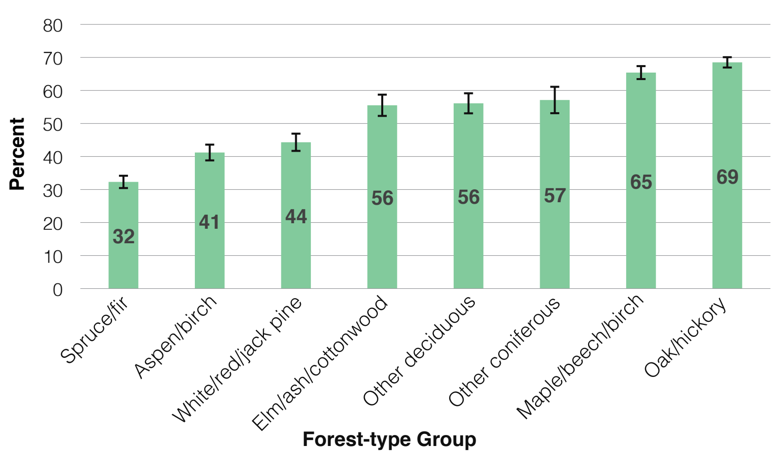


Figure 11.—Percentage of forest land with moderate or high ungulate browse impacts by forest-type group, Midwest and Northeast, 2017. Error bars represent 68 percent confidence intervals.

# DISCUSSION

Although it was not feasible to make direct quantitative comparison with Leopold and others' map due to differences in methodology, it is clear that regions identified by Leopold and his colleagues remain as challenges for regeneration management. Oak/hickory and maple/beech/birch are under more browse pressure than the other forest-type groups. The proportion of forest land with moderate or high browse impacts for the other forest-type groups ranged from 32 to 57 percent, further supporting the notion that ungulate-compatible silviculture, such as prescribed fire, control of competing vegetation, and fencing, has become a major thrust for managers in the Midwest and Northeast. A synoptic review of existing silvicultural systems in the context of browse pressure clarifies the spectrum of options available to overcome challenges to successful regeneration management. Management decisions for specific forest stands depend on the mixture of stress factors and taxa desired for the regeneration component.

The two most prevalent forest-type groups in the study region (oak/hickory and maple/beech/birch), as well as aspen/birch, spruce/fir, and white/red/jack pine forest-type groups, are discussed next to illustrate management options for systems under browse stress.

## OAK/HICKORY FOREST-TYPE GROUP

Successful regeneration of the oak/hickory forest-type group is a prime example of the role of forest management in overcoming regeneration obstacles. Most oak/hickory forest land in Missouri has relatively low moderate or high browse impacts, though impacts were higher in Ohio, Indiana, and Illinois, and the Mid-Atlantic and New England subdivisions. Oaks, hickories, and some associates share traits that work against stand replacement efforts, such as high palatability and intermediate shade tolerance or shade intolerance. They tend to grow where large-gap disturbances (fire) are

White-tailed deer herd. Photo by Sin H. Ling, Winter Wildlife NJ, used with permission.

Forest ground flora. Photo by William H. McWilliams, USDA Forest Service.

uncommon. These characteristics create advantages for maples and other taxa that are less palatable, are more shade tolerant, and can regenerate in small gaps. Ungulate-compatible measures to overcome these conditions are large-gap disturbance, prescribed fire, control of competing vegetation, and deer impact mitigation.

The shelterwood system has been a successful technique for establishment and development of advance regeneration in oak/hickory forests when used along with related prescriptions: fencing, herbicide, or prescribed fire (Brose et al. 2008, 2014). Shelterwood harvests create large gaps, and burning controls competing vegetation by eliminating more fire-sensitive species, such as red maple (Fei et al. 2011, Raeker et al. 2011). Chemical or mechanical control of competing vegetation may also be required to foster microsites favorable to germination and provide increased growing space for seedlings. Some advantages of shelterwood systems are the flexibility to provide available light by managing stand density through one or more harvests, control of seed tree composition, development of conditions to promote the establishment of advance regeneration, and development of desirable regeneration from advance reproduction, stump sprouts, and seed.

In areas that have a history of browsing, recalcitrant understory vegetation can inhibit seedling establishment and development (Royo and Carson 2006). This condition requires control by using herbicides, brush cutting, and release cuts. These prescriptions can be enhanced by fencing or caging crop trees. Oak/hickory stands in the woodlands and savannas of the Plains States with abundant reproduction are characterized by unique conditions of diverse flora and fauna, and greater vegetative biomass in the understory. These natural features provide alternative food for herbivores, which helps decrease pressure on young seedlings (Dey and Kabrick 2015).

## MAPLE/BEECH/BIRCH FOREST-TYPE GROUP

Maple/beech/birch forest land is most common in the northern ecological subdivisions, where the native ranges of deer and moose overlap. Woody vegetation food choices of deer and moose are similar, suggesting the possibility of competition between these herbivore species (Hunter 1990). However, their distribution is more influenced by other habitat factors; deer prefer shelter, such as forest edges, and moose are comfortable in a wide range of habitats with a range extending farther northward (Kearney and Gilbert 1976). Both deer and moose alter their seasonal browse patterns as they seek protection during extreme climatic events. For example, deer favor dense forest patches often dominated by conifers during snow storms or extreme cold weather. Heavy concentrations of ungulates can cause localized suppression of conifers and other species that serve as winter food sources, regardless of overall ungulate abundance on the landscape (Witt and Webster 2010). Increasing available light for development of shade-intolerant species by forest thinning or harvesting is a practical goal, but it is crucial to use opening sizes and manage light levels so that they meet the physiological needs of desired species and promote growth without encouraging competing vegetation (see Kern et al. [2016] for details).

Although the northern subdivisions generally have lower probabilities of browse impacts, there are areas with probabilities of 31 percent to 60 percent for moderate or high impacts where forest managers will need to be cognizant of local conditions. Increases in moose populations in the northern part of the New England subdivision beginning in the late 1970s have resulted in concentrated areas of high pressure in Maine, New Hampshire, and Vermont, particularly for deciduous species (Andreozzi et al. 2014). Moose populations have also expanded into portions of southern New England, leading to localized impacts on the regeneration of eastern hemlock and maple (Faison et al. 2010). Declines in moose have been reported in the news for the Great Lakes region, but peer-reviewed findings have not confirmed these reports. Current anecdotal evidence suggests that a warmer climate in conjunction with an increase in occurrence of the moose tick (*Dermacentor albipictus*) is a related concern due to moose mortality caused by anemia, particularly along the southern edge of the ungulate's range. Future trends in moose population density will ultimately determine the role of this herbivore in the development of forest understories.

Maple/beech/birch regeneration management activities are made complicated by differences in tree-seedling palatability and shade tolerance (Nyland 2002, Oliver and Larson 1996, Smith et al. 1997). Gap-based silviculture allows tailoring of harvest gaps to address these complications, but requires minor or major adjustments to business-as-usual management practices due to browsing. The selection of mitigation practices depends on forest type, condition, and browse levels. For instance, managers interested in regenerating a particular species within closed-canopy forests typically control available light by manipulating canopy openness to favor the shade tolerance of regenerating seedlings and improve the probability of gaining a dominant or codominant canopy position in the future forest (Kern et al. 2016). A business-as-usual practice may be to create canopy gaps of 33 to 66 feet in diameter to establish pockets of shade-intolerant yellow birch (*Betula alleghaniensis*) regeneration within closed-canopy maple stands. Current conditions of moderate or high browse impacts in the region may thwart implementation of this management strategy because yellow birch seedlings are a browse-preferred species and small-statured seedlings are within an ungulate's reach. Under these conditions future canopy dominants are more likely to be species that are browse resistant rather than shade intolerant (Kern et al. 2012).

Ungulate mitigation efforts could include gap-level protection until the pocket of regeneration outgrows the reach of ungulates, such as use of temporary fencing, repellents, or bud caps (MacGowan et al. 2004, Ward and Mervosh 2008). In most cases, these gaps are dispersed and numerous across stands, which means gap-level mitigation measures may not be cost effective.

As on oak/hickory forest land, large harvest areas are used to foster tree-seedling densities that exceed the feeding capacity of the local ungulate population. Maintaining high-density mixtures of preferred and nonpreferred species has been suggested as a way to confer associational resistance to browse-preferred species (Herfindal et al. 2015). Leaving unmerchantable tops and limbs minimizes nutrient loss and creates shelters for seedling development and impediments to browsers if slash is piled (Leak et al. 2014, Van Ginkel et al. 2013). Managers can also consider landscape-scale ungulate mitigation by focusing regeneration management in stands where nonforest sources of food are available to divert browsers away from preferred browse species or, conversely, focus regeneration efforts far from known ungulate concentrations, such as in deer wintering areas (Millington et al. 2010).

## OTHER FOREST-TYPE GROUPS

The northern subdivisions have a large proportion of the study region's aspen/birch, spruce/fir, and white/red/jack pine forest land. Unique regeneration management options are available for these forest-type groups when under deer or moose browse pressure. Managers need to consider not only palatability, shade tolerance, and fire resistance, but also the role of target taxa in succession (pioneer or climax). The choice of silvicultural prescriptions may include natural regeneration, planting, or a combination of both to ensure enough seedlings for adequate regeneration. In areas of high browse impact, techniques such as fencing, tree cages, and others mentioned earlier should be used according to browse level and species palatability.

# CONCLUSIONS

Results of this study underscore three challenges for regeneration management of midwestern and northeastern forests under browse stress. First, browse impacts have extensive and long-term implications. Large ungulates still impede regeneration management in problem areas identified by Leopold and colleagues 70 years ago. Leopold did not predict that control or reduction of large ungulates would become a perennial challenge, but he did correctly anticipate that problem areas would expand as now apparent in the Central/Plains, Mid-Atlantic, and New England subdivisions. Since then, moose have repopulated native ranges and reached irruptive levels in some areas of New England (Wattles and DeStefano 2011). As noted by DeGraff and Yamasaki (2000), populations of such predators as gray wolf (*Canis lupus*), coyote (*Canis latrans*), black bear (*Ursus americanus*), and bobcat (*Lynx rufus*) have also increased since Leopold and colleagues' study.

Second, less palatable tree species will continue to have a competitive advantage during the regeneration stage, potentially resulting in a future canopy composition that is different from the existing canopy-dominant species. Composition of new plant assemblages of browse-resistant plants will need to be identified, studied, and included in management planning as appropriate (Lugo 2015). Managers may need to modify desirable species lists and accept new taxa and assemblages as surrogates for native taxa. Where possible, it is important to identify and promote existing native species to ensure sustainability of forest values that the public has come to expect, such as high-canopy taxa, aesthetics, wildlife, nontimber forest products, and marketable wood.

In general, regeneration of deciduous and coniferous forests dominated by taxa of intermediate shade tolerance or shade intolerance require competitive advance regeneration, adequate light, control of competing

Young red spruce (*Abies rubens*) and fir *(Abies balsamifera*). Photo by William H. McWilliams, USDA Forest Service.

vegetation, and protection of young seedlings from browse damage. Study results identified oak/hickory and maple/beech/birch forest-type groups as having the most forest land under browse stress. Of particular concern is the restoration of large-seeded taxa with intermediate to low shade tolerance that rely on abundant light during the establishment stage of regeneration, such as oaks, hickories, and walnuts (*Juglans* spp.). Pine-dominated forests in stressed areas will require examination of local browse levels and selection of appropriate prescriptions for natural and plantation management.

Third, even though the principle that early stand management determines future forest condition is axiomatic, it takes on a new dimension for forests under browse stress given the empirical results presented here. Monitoring composition, structure, and browse will be critically important for success. Planning for regeneration management is made difficult by the interactions of multiple factors, such as the size and condition of the forest tract, dominant tree species, degree of alien plant or pest intrusion, and the population dynamics of the browsers, as influenced by birth rate and losses from predation, disease, and starvation. As large-ungulate browsing delays or curtails regenerative potential, recovery of forest understories can take from 20 to 50 years depending on conditions, varies from full to partial restoration, and may never be achieved (Hobbs 1996, Latham et al. 2005, Nuttle et al. 2014, Rooney et al. 2004).

Some practical concepts from Pennsylvania's long history of browse stress that have been successful in reducing landscape-scale impacts are: managing browsing; monitoring and controlling local browser populations; coordinating among owners, agencies, and other authorities; and implementing silvicultural prescriptions compatible with browse impacts (McWilliams et al. 2017). Cooperation between wildlife and forestry agencies has a proven track record in the Mid-Atlantic region; for example, landscape-level herd management has improved the balance between deer and forest habitat in Pennsylvania (Rosenberry et al. 2009). As new information becomes available, science-based adaptive management will best ensure success in achieving management goals.

This study has demonstrated that mitigation of the effects of large-ungulate browsing will require forest policymakers and managers to be diligent over the long term in focusing on management of local conditions using the suite of available silvicultural tools and yet undiscovered approaches. Results of this study begin to fill geospatial knowledge gaps and address policy and management realities for the study region. The browse-impacts visualization thus generated illustrates the need for consistent empirical-based monitoring of ungulate effects and vegetation over time and on broad spatial scales. Global climate variability has recently become a primary impetus for long-term planning exercises in natural resource planning and management, but the results of this paper demonstrate that the pervasive impacts of historical and current browsing will also be a primary driver of future forest conditions in the Midwest and Northeast.

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Browse of forest understory vegetation by deer and other large ungulates alters ecosystem processes, making it difficult to regenerate forest land in herbivory-stressed areas. Seventy years ago, Aldo Leopold identified problem areas in the United States where overpopulation of white-tailed deer (*Odocoileus virginianus*) was likely to lead to overbrowsing of nutritive plants. Species of plants with little or no nutritive value would thereby gain a competitive advantage. Recent measurements of browse impacts on regionwide forest inventory plots in the midwestern and northeastern United States provide the opportunity to review the work of Leopold and others. A visualization of the probability of browse impact levels that warrant consideration during regeneration planning is presented for comparison to historical maps.

Currently, 59 percent of the 182.4 million acres of forest land inventoried in the Midwest and Northeast was estimated to have moderate or high browse impacts. The Mid-Atlantic region had the highest proportion of forest land with moderate or high browse impacts (79 percent). The oak/hickory (*Quercus/Carya*) and maple/beech/birch (*Acer/Fagus/Betula*) forest-type groups each had percentages of forest land with moderate or high impacts above the regional average, 69 percent and 65 percent, respectively. The problem areas described by Leopold and others persist and new areas have emerged in the Central/Plains, Mid-Atlantic, and New England States.

The study findings confirm three realities of forest regeneration management for forests under herbivory stress in the Midwest and Northeast: 1) The scope and persistence of large-ungulate herbivory has long-term wide-ranging implications for regeneration management; 2) less palatable tree species will continue to have a competitive advantage during the regeneration phase and are likely to be different species from the current canopy dominants; and 3) successful regeneration management of these forests requires more emphasis on ungulate-compatible prescriptions, novel approaches, and adaptive science.

**KEYWORDS:** browse map, tree regeneration, wildlife habitat, white-tailed deer, forest understory, forest monitoring, forest sustainability

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