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Habitat Relations

Current and Projected Abundance of Potential Nest Sites for Cavity-Nesting Ducks in Hardwoods of the North Central United States

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ABSTRACT Clearing of hardwood forests was widespread in the north central region of the United States at the turn of the 20th century, but largely subsided by the 1920s. Hardwood trees in the region have since regenerated and matured into sizes capable of producing nest cavities suitable for cavity-nesting ducks. We estimated regional nest-site abundance for cavity-nesting ducks during 2008, 2018, and 2028 from cavity density and tree-abundance estimates obtained at 4 hardwood forest sites in conjunction with Forest Inventory and Analysis data and tree-growth modeling software from the United States Forest Service (Forest Vegetation Simulator). Land cover data were used to determine area of hardwood forests ≤0.5 km, 0.5–1 km, 1–1.5 km, 1.5–2 km, and >2 km from wetlands and open water available to cavity-nesting ducks. We estimated 13.2 million, 17.0 million, 19.0 million, and 20.1 million potential duck nest cavities available ≤0.5 km, ≤1 km, ≤1.5 km, and ≤2 km of water, respectively, in the region and predicted nest cavity abundance will increase 41% from 2008 to 2028. Hardwood forests in Indiana, Michigan, Ohio, and Wisconsin currently have the highest abundances of potential nest sites, but cavity-bearing forests in Minnesota, Michigan, and Wisconsin were more commonly proximate to wetlands and open water. Because current and future estimates indicate sufficient nest sites to support growing cavity-nesting duck populations in the north central United States, we recommend regional management efforts focus on protecting, restoring, and maintaining quality wetlands in proximity to hardwood forests.

KEY WORDS cavity-nesting ducks, hardwood forests, Midwest, natural cavities, wetlands.

Widespread forest clearing at the turn of the 20th century, in conjunction with unregulated market hunting, caused sharp declines in cavity-nesting duck populations in eastern North America (Phillips 1925, 1926; Bellrose 1980). Forest clearing of that scale was largely curtailed by the 1920s, and forests have regenerated and matured in much of the United States since that time (Smith et al. 2009). Re-growth of forests and establishment of duck harvest regulations appear to have positively influenced cavity-nesting duck populations (Bellrose 1980, Bellrose and Holm 1994).

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Wood ducks (*Aix sponsa*), hooded mergansers (*Lophodytes cucullatus*), and common goldeneyes (*Bucephala clangula*) are cavity-nesting ducks occurring in the north central United States during the breeding period of the annual life cycle (Fig. 1). Although estimates of abundance for cavity-nesting ducks are difficult to obtain due to poor detection rates when surveying ducks in forested areas, breeding season indices suggest upward population trends since the mid-1960s in the north central United States (Sauer et al. 2008).

Cavity-nesting ducks will readily nest in artificial nest sites (boxes) but most often use natural cavities (Bellrose and Holm 1994, Dugger et al. 1994, Eadie et al. 1995). Cavity formation is considered a spatially stochastic process caused by tree injury (Fan et al. 2003, 2004*a*, *b*), but individual tree age and diameter at breast height (dbh) are positively correlated with cavity production (Goodburn and Lorimer 1998, Fan et al. 2003). Mature hardwood trees have more natural cavities for cavity-nesting ducks than younger hardwoods and conifers (Bellrose and Holm 1994), and live trees account for substantially more suitable

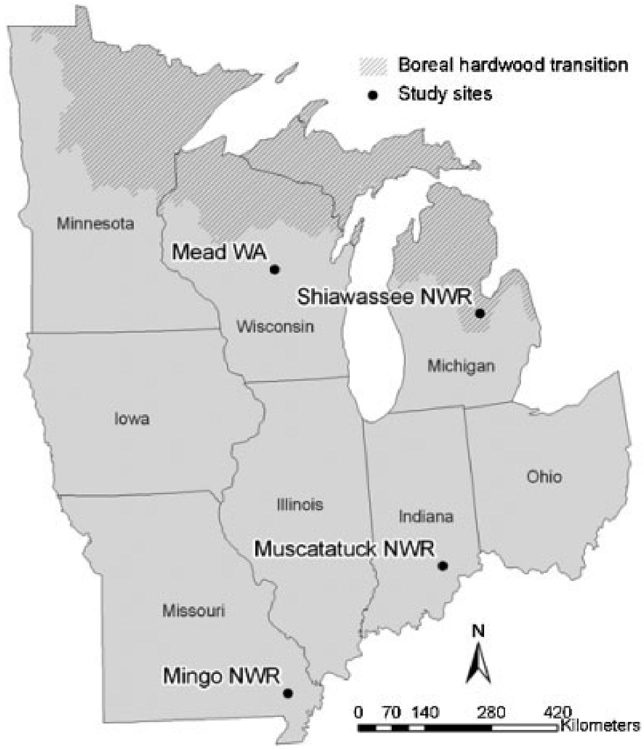

Figure 1. Location of sites used to gather suitable cavity/tree data in the north central United States, 2007–2008. Wood ducks and hooded mergansers breed throughout the region whereas common goldeneye breeding range approximates the Boreal Hardwood Transition.

nest cavities than dead trees (72–100%; Bellrose and Holm 1994, Yetter et al. 1999, Zwicker 1999, Denton 2009).

Total forest area (hardwood and conifer dominated forests combined) has increased slightly from 34.1 million ha to 35.1 million ha from 1953 to 2007, and although reliable data on hardwood-dominated forest coverage do not date back to 1953, a slight increase (0.5%) was recorded from 1997 to 2007 in the north central region (Forest Inventory and Analysis Program [FIA] 2007, Smith et al. 2009). Hardwood-dominated forests make up approximately 84% of forest coverage and 25% of total land area in the region (FIA 2007). Average annual volume growth of hardwood trees in the north central United States has exceeded annual volume harvest during the past 50 years, and this trend is expected to persist as trees mature in the region during the next 50 years (Shifley and Sullivan 2002, FIA 2007). All states in the north central region (Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio, and Wisconsin) experienced a substantial increase (232–372%) in total volume of hardwood growing stock since 1953, with the volume of large ($\geq$28 cm dbh) hardwood growing stock increasing from 0.48 billion to 1.66 billion m^3 between 1953 and 2007 (Smith et al. 2009). The increased abundance of large hardwood trees in the region has the potential to produce more duck nest cavities than it has in over a century.

Wood ducks are the most common cavity-nesting duck species and have been used as a focal species for waterfowl habitat conservation planning by the Upper Mississippi River and Great Lakes Region Joint Venture (Soulliere et al. 2007). The Joint Venture's regional conservation strategy assumes tree-cavity nest sites do not limit wood duck populations from realizing population goals at the regional scale; however, the strategy also calls for testing planning assumptions. The objective of this study was to test the planning assumption that nest sites are not limiting cavity-nesting duck populations. We determined the abundance, distribution, and tree characteristics of suitable duck nest sites to inform conservation decisions regarding habitat for cavity-nesting ducks in the north central United States. In addition to current abundance of suitable duck nest sites, we predicted future abundance using nest-cavity density and tree data we collected, region-wide United States FIA data, forest-modeling software from the United States Forest Service, and a Geographic Information System (GIS).

STUDY AREA

We modeled cavity abundance for the north central United States (U.S. Forest Service North Central Region, U.S. Fish and Wildlife Service Region 3) including the states of Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio, and Wisconsin. We use the terms north central region and north central United States to refer to the same 8-state area. Region-wide measures of forest composition on both public and private lands were obtained from FIA data collected by the United States Forest Service (Smith 2002). To generate estimates of suitable duck nest-cavities for each tree species and tree size class, we collected cavity and tree data at 4 study sites within the study area: Muscatatuck National Wildlife Refuge (NWR) in Indiana, Mingo NWR in Missouri, Shiawassee NWR in Michigan, and a study site encompassing Mead State Wildlife Area and bordering private lands in Wisconsin (Mead WA). We sampled upland and bottomland forests at each site to estimate cavity densities in tree species occurring in both mesic and hydric conditions. Our forest samples included all primary hardwood forest types found in the north central region (i.e., oak-hickory, maple-American beech-birch, aspen-birch, elm-ash-cottonwood, oak-pine, and oak-gum-cypress; Shifley and Sullivan 2002), most hardwood species capable of growing to cavity-producing sizes (Keyser 2008*a*, *b*), and all important nest cavity-producing hardwood species known to occur in the region (Bellrose and Holm 1994, Roy Nielsen et al. 2007).

Muscatatuck NWR is located in Jackson and Jennings County in southern Indiana (Fig. 1). The refuge was established in 1966, when land cover consisted primarily of agriculture (Muscatatuck National Wildlife Refuge 2007). Currently, Muscatatuck NWR encompasses 3,180 ha including upland and bottomland hardwoods (2,400 ha), croplands (390 ha), and marshes, lakes, and ponds (390 ha). Shiawassee NWR, in Saginaw County Michigan, was established in 1953 after the land had been logged, mined, and converted to agriculture during the early part of the century (Shiawassee National Wildlife Refuge 2007; Fig. 1). The refuge now spans 3,900 ha and is comprised of forests (1,700 ha total; 1,400 ha in hardwoods), wetlands (1,500 ha), grasslands (230 ha), and croplands (470 ha).

Mingo NWR is located in Stoddard and Wayne Counties, in southeast Missouri (Fig. 1). The refuge was created in 1944 to re-establish forests cleared during the early part of the century (Mingo National Wildlife Refuge 2007). During our study, it contained 8,150 ha with 6,070 ha of forests (5,200 ha bottomland and upland hardwoods), 200 ha of croplands, 290 ha of moist-soil units, 190 ha of grasslands, and 1,400 ha of wetlands. Our fourth study site included Mead WA and surrounding public (i.e., county owned) and private lands in Marathon, Wood, and Portage counties in central Wisconsin (33,200 ha; Fig. 1). The wildlife area itself, where the majority of sampling took place, was gifted to the state in 1959 to establish a wildlife refuge following forest clearing and wetland draining for agriculture during the late 19th century and early 20th century and a failed proposal to convert the area into a reservoir in the 1930s (Mead State Wildlife Area 2007). At present, Mead WA contains 13,400 ha of wetlands (5,700 ha), grasslands (2,400 ha), and upland and floodplain forests (5,300 ha). All public and private hardwood-dominated forests (8,000 ha) within an area of 33,200 ha centered on Mead WA were included. The remaining land cover consisted primarily of agriculture and non-hardwood forests. All aforementioned study site land cover areas (ha) are approximate.

METHODS

Determining Cavity Distribution Among Trees

We sampled individual trees to arrive at tree-based estimates of suitable cavity production (e.g., suitable nest cavities/species and dbh size class), rather than stand-based estimates. We collected suitable nest-cavity density and tree data among species and size classes of hardwoods large enough to produce suitable cavities ($\geq$28 cm dbh; Lowney and Hill 1989, Lee 1991, Havera et al. 1995, Ryan 1995) from 99 randomly selected 0.5 ha plots at 4 study sites in the region: Shiawassee NWR (2,180 trees in 25 plots), Muscatatuck NWR (1,565 trees in 25 plots), Mingo NWR (2,034 trees in 25 plots), and Mead WA (1,326 trees in 24 plots). Two-person teams visited study sites during the winters of 2006–2007 (Indiana, Michigan) and 2007–2008 (Missouri, Wisconsin) after leaf-off to ensure the highest possible cavity detection rates. We delineated sample plots in a 0.5 ha square (70.7 m $\times$ 70.7 m) around plot center. We used a Biltmore stick or dbh tape to determine the diameter of all trees $\geq$28 cm dbh. Crewmembers independently and then collectively searched all trees in the plot with binoculars. When we observed potentially suitable cavity entrances from the ground, we ascended to cavities using the single-rope technique (Perry 1978) or climbing spikes. We also noted and later assessed any additional cavity entrances detected while elevated. To estimate suitable cavity detection probabilities, we climbed $\geq$4 randomly selected trees to $>$12 m at each of 10 plots at Mead WA and Mingo NWR to identify suitable cavities that may have been missed during ground searches. We used minimum and maximum cavity suitability criteria from the literature based on actual duck nests: 6 cm $\times$ 6 cm (28 cm^2) minimum-entrance dimensions (Zwicker 1999), 2,325 cm^2 maximum-entrance area (Robb 1986), 0–500 cm cavity depth, $\geq$0.9 m cavity height (Ryan 1995, Roy Nielsen et al. 2007), and minimum platform dimensions of 14 cm $\times$ 15 cm ($\geq$165 cm^2; Haramis 1975). We also considered cavities unsuitable if water pooled on the platform or if a hen would be completely exposed to predators.

We focused on hardwoods and did not sample conifers due to their relatively low importance to cavity production (C. Gayle, U.S. Fish and Wildlife Service, unpublished report; Bellrose and Holm 1994, Vaillancourt et al. 2009), although some northern areas of the region were dominated by conifers. We only included individual tree species representing $\geq$1% of total trees in our analyses, except when less common species were important for potential nest-cavity production (i.e., they accounted for $>$5% of cavity trees). All other uncommon ($<$1% of total) hardwood trees were grouped into a single category labeled "Other species" (Table 1). We then determined the number of suitable nest cavities for each tree species and dbh size class to obtain tree-based estimates of suitable cavity production.

Forest Composition From Regional Forest Inventory and Analysis Data

We used FIA data (Smith 2002, FIA 2007) and Forest Vegetation Simulator software (FVS; U.S. Forest Service, Fort Collins, Colorado; Dixon 2002) to model cavity abundance across the north central region. The FIA program collects, analyzes, reports, and distributes data on the extent, content, and condition of United States forests annually on both public and private land (Smith 2002, FIA 2008). Plots are distributed throughout the United States (1 plot/2,429 ha) and plots are sampled at an intensity of 10–20% per state per year (FIA 2008). To protect plot integrity and private landowners, exact plot coordinates are either fuzzed, meaning the location given by FIA is $\leq$1.6 km of the actual location (most often $<$0.8 km), or swapped, meaning the location given is of a similar plot that is matched for forest type and stand size within the same county, which occurs $<$10% of the time (McRoberts et al. 2005, FIA 2008). Fuzzed and swapped plots are highly correlated with estimates derived from plots using actual locations when areas of interest are large ($\geq$20-km radii [125,664 ha]; Lister et al. 2005, McRoberts et al. 2005).

Plots in FIA cover a 0.4047 ha area (FIA 2008). Sampling is carried out using 4 7.32-m radius subplots for trees with $\geq$12.7 cm dbh and 4 2.07-m radius microplots for trees with $\leq$12.7 cm dbh, and a tree expansion factor equal to the inverse of total subplot or microplot area sampled is used to determine the number of trees a sample tree represents per plot (FIA 2008). Tree species, dbh, trees/ha (TPH), and location obtained or derived from FIA plots comprised the initial conditions of our model.

Forecasting With Forest Vegetation Simulator

Forest Vegetation Simulator was designed to forecast stand dynamics in the United States through an individual-tree, distance-independent growth and yield model able to

Table 1. Suitable nest cavities/tree for ducks by species and size class based on combined data from Muscatatuck National Wildlife Refuge (NWR), Shiawassee NWR, Mingo NWR, and Mead Wildlife Area. Note: Detection probabilities were high (98%; Denton 2009). Size groups with equal cavity/tree values for a species indicates we combined cavities and total trees in those groups.

	Diameter at breast height (cm)					
Species	**28–39**	**40–49**	**50–59**	**60–69**	**70–79**	**≥80**
Acer rubrum	0.000	0.029	0.054	0.054	0.054	0.054
A. saccharinum	0.008	0.015	0.016	0.020	0.057	0.057
A. saccharum	0.011	0.025	0.056	0.056	0.056	0.056
Fagus grandifolia	0.000	0.143	0.143	0.222	0.222	0.333
Quercus alba	0.000	0.010	0.010	0.010	0.010	0.010
Q. lyrata	0.000	0.010	0.010	0.010	0.010	0.010
Q. palustris	0.005	0.014	0.014	0.014	0.014	0.014
Q. phellos	0.011	0.011	0.011	0.011	0.011	0.011
Q. rubra	0.000	0.017	0.017	0.017	0.017	0.017
Liquidambar styraciflua	0.005	0.010	0.021	0.045	0.083	0.083
Sassafras albidum	0.105	0.125	0.125	0.125	0.125	0.125
Liriodendron tulipifera	0.006	0.006	0.006	0.006	0.006	0.006
Nyssa sylvatica	0.100	0.273	0.273	0.273	0.273	0.273
Fraxinus pennsylvanica	0.002	0.019	0.019	0.019	0.019	0.019
Platanus occidentalis	0.000	0.061	0.061	0.061	0.061	0.061
Populus tremuloides	0.002	0.002	0.002	0.002	0.002	0.002
Tilia americana	0.012	0.012	0.012	0.012	0.012	0.012
Ulmus americana	0.000	0.048	0.048	0.048	0.048	0.048
Other species	0.002	0.003	0.003	0.003	0.003	0.003

simulate tree growth under various stand structures, forest types, and stand diversity (Dixon 2002, Crookston and Dixon 2005). The program models growth and mortality using complex equations which incorporate numerous variables (e.g., potential diameter annual growth, crown competition, crown ratio, annual diameter growth, height growth, typical mortality, and density-related mortality; Dixon 2002, Crookston and Dixon 2005), site-specific coefficients, and species-specific coefficients (Dixon 2002; Keyser 2008*a*, *b*). The simulator accounts for geographic differences in species-specific tree growth and mortality with imbedded equations called variants (Dixon 2002). We used the Central States variant for plots in Illinois, Indiana, Iowa, Missouri, and Ohio and the Lake States variant for plots in Michigan, Minnesota, and Wisconsin (Keyser 2008*a*, *b*).

We used current north central region FIA data converted to FVS-ready files by the United States Forest Service. We filtered the files to include only FIA plots with hardwood trees because we only sampled and estimated cavity abundance in forests containing hardwoods. All trees from FIA plots were grown in each state using FVS-base growth models using the SUPPOSE interface of FVS (Dixon 2002). Trees were grown in 10-year intervals out to year 2028 starting with 2008. We felt 20 years was adequate time to illustrate the effect of forest maturation on potential nest-cavity abundance for ducks, plus accuracy of results would be less influenced by model limitations and assumptions than with a longer period. Simulations resulted in a regional database of structural variables for all live trees in each FIA plot for 2008, 2018, and 2028. The 2008 output depicted forest conditions as they currently stand (i.e., harvested and non-harvested), but trees in future simulations (2018 and 2028) could only be removed by natural mortality since our model did not attempt to predict future harvest across the region.

Forest Vegetation Simulator reports natural mortality of trees/ha (MTPH) at the conclusion of each 10-year interval. However, it does not report the exact year dying trees are removed from TPH (live inventory) or whether dead trees had fallen (i.e., no value to cavity-nesting ducks) during the 10-year time interval. Therefore, we excluded dead trees and we only included live trees standing throughout the entire 10-year interval in future nest-cavity estimates.

We did not include regeneration of trees in our simulations because few, if any trees in the region would be capable of growing from seed to ≥28 cm dbh during a 20-year period (Burns and Honkala 1990). Only trees with a starting size ≥2.5 cm dbh from current FIA data were grown in our simulations since FIA does not include seedlings (<2.5 cm dbh) with tree data. After simulations created outputs for 2008, 2018, and 2028 in database format, we removed all conifers and all hardwood trees <28 cm dbh. We excluded hardwood trees <28 cm dbh from the output because 28 cm dbh is considered the minimum size capable of producing suitable nest cavities for the 3 duck species common to the region (Lowney and Hill 1989, Lee 1991, Havera et al. 1995, Ryan 1995).

We sorted trees from FIA plots by species and size class and applied the appropriate cavities/tree value to each tree (Table 1). We multiplied this product by the TPH value and summed the result for each tree to derive cavities/ha for each plot. We joined this file to an FIA table containing plot location and created 3 database files (2008, 2018, 2028) containing plot number, cavities/ha, latitude, and longitude. We converted these files to a point shapefile for GIS analysis.

GIS Methods

We used ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA) for all GIS mapping and processing. We mapped each point containing tree species composition and cavity density. We pooled and mapped points by Bailey's Ecoregion sections (Bailey 1976), which were large enough (153,535–12,960,089 ha) to nullify any possible bias caused by fuzzed and swapped FIA point locations (McRoberts et al. 2005). Bailey's Ecoregion sections, hereafter sections, are part of a hierarchical system developed for the United States Forest Service (Bailey 1976). Bailey's Ecoregions represent landscapes of common climatic and vegetation characteristics, which we preferred over mapping by political boundaries (e.g., state) having no ecological basis. The north central region contains all or part of 27 sections.

To estimate nest-site abundance for cavity-nesting ducks, we first determined the total area of forest proximate to wetlands and open water (i.e., rivers, streams, and lakes) which could provide suitable brood-rearing habitat or corridors to suitable habitat. We primarily used the National Land Cover Database 2001 (NLCD; Homer et al. 2007) and to a lesser extent Gap Analysis Program data (GAP; Scott et al. 1993) for these analyses. The NLCD was the only digital spatial data with standardized forest and wetland classifications across all states in the region. Using NLCD, we determined the total area of hardwood and mixed hardwood forests. Specifically, we used codes 41 (Deciduous Forest), 43 (Mixed Forest), and 90 (Woody Wetlands) to map all areas containing hardwoods within the region. We assumed these mapped areas contained trees capable of producing cavities since the NLCD indicated deciduous forest and mixed forests were areas generally dominated by trees >5 m tall. Woody wetlands included forest and/or shrubland vegetation where the soil was periodically saturated with or covered with water. A few areas in southern portions of the region mapped as woody wetlands by NLCD may have contained extensive common buttonbush (*Cephalanthus occidentalis*) coverage and no hardwood trees capable of producing cavities, but we assumed that these areas generally contained trees large enough to have cavities since common buttonbush is most often associated with cavity-producing bottomland hardwood species (e.g., overcup oak [*Quercus lyrata*], river birch [*Betula nigra*], swamp cottonwood [*Populus heterophylla*], and water tupelo [*Nyssa aquatica*]; Burns and Honkala 1990). Woody wetlands made up a small proportion (8%) of hardwood forest cover, further limiting impacts of this assumption. Additionally, because NLCD mapped coniferous bogs (located in northern extremes of the region) as woody wetlands and our focus was on hardwoods, we used GAP data from Minnesota, Wisconsin, and Michigan to exclude conifer-dominated woody wetlands, which occur in those states. Areas removed from the forest mapped by NLCD included: Minnesota GAP landcover codes 11 (Lowland Evergreen Shrub), 26 (Lowland Black Spruce), 29 (Stagnant Tamarack), 30 (Lowland Northern White Cedar), 31 (Stagnant Northern White Cedar), and 32 (Stagnant Conifer); Wisconsin GAP landcover codes 219 (Broad-leaved Evergreen Wetland), 220 (Needle-leaved Evergreen Wetland), 229 (Coniferous Wetland), 230 (Black Spruce Wetland), 231 (Tamarack Wetland), and 232 (Northern White-Cedar); and Michigan GAP landcover codes 612 (Lowland Coniferous Forest). The resulting file contained the estimated distribution and quantity of all areas containing mature hardwood trees, hereafter hardwood forests, in the north central region. The distribution of north central region FIA plots containing mature hardwoods ($n = 18{,}965$) followed our hardwood forest coverage closely, lending evidence to the accuracy of our estimated hardwood forest coverage.

We then mapped wetlands and open water, which could serve as brood-rearing habitat or corridors to brood-rearing habitat, hereafter water, using the NLCD. We used landcover codes 90 (Woody Wetlands), 95 (Emergent Wetlands), and 11 (Open Water) to initially map water. We removed coniferous bogs from Woody Wetlands as before using GAP data. We calculated Euclidian distance to water for all areas in the region.

Cavity-nesting duck species use cavities at varying distances from water (Bellrose and Holm 1994, Dugger et al. 1994, Eadie et al. 1995), so we determined cavity abundance from ≤0.5 km, 0.5–1 km, 1–1.5 km, 1.5–2 km, and >2 km of water for the region. We identified the amount of hardwood forests at ≤0.5 km, 0.5–1 km, 1–1.5 km, 1.5–2 km, and >2 km from water to determine coverage of hardwood forests in proximity to water per section. After we determined the location of all hardwood forests, wetlands, and open water, we calculated the percentage of total forest area ≤0.5 km, ≤1.0 km, ≤1.5 km, and ≤2.0 km from water for the region.

We calculated mean nest cavities/ha within all hardwood forests for each section at each time interval (2008, 2018, 2028) based on simulated data for all plots falling within that section. We made comparisons of cavities/ha within hardwood forests in the region between consecutive estimates (i.e., 2008 and 2018; 2018 and 2028) with 2-tailed paired t-tests. We used an α-level of 0.05 to determine significance of t-tests. We multiplied mean nest cavities/ha for each section by the total area of all hardwood forests and by the area of hardwood forests within ≤0.5 km, 0.5–1 km, 1–1.5 km, 1.5–2 km, and >2 km of water to generate potential abundance of nest cavities for each time interval/section. We summed the section totals to derive regional estimates of potential nest cavity abundance.

We summed the number of potential cavities produced by each tree species and divided by the total number of cavities produced by all tree species combined based on FVS outputs for 2008–2028. This process generated the proportion of cavities produced by individual tree species within the region for 2008, 2018, and 2028. We performed the same procedure for dbh size classes (28–39 cm, 40–49 cm, 50–59 cm, 60–69 cm, 70–79 cm, ≥80 cm) at each time interval producing a proportion of cavities produced by a given dbh size class for 2008, 2018, and 2028.

Assumptions

We made several assumptions when predicting regional abundance of suitable nest cavities with FVS simulations and GIS analysis. We state them explicitly to improve transparency and interpretation of the results and discussion.

1. Cavity formation rates of trees at each of the sites we measured are representative of cavity formation rates of the same tree species in the same size class across the region (i.e., individual trees on public lands have the same probability of forming cavities as individual trees on private lands).
2. Tree removal by future harvest was not included, but volume removed will not surpass volume growth.
3. Literature-obtained values of minimum tree size (≥28 cm dbh) to house a cavity suitable for nesting were accurate for cavity-nesting species common to the region.
4. Coniferous trees contribute a small proportion of suitable nest cavities for cavity-nesting species common to the region relative to the contribution of cavities by hardwoods in the region, thus a focus on hardwoods is conservative, yet captures the vast majority of the expected changes.
5. Growth from seedlings over the 20-year simulation period would not result in new nest-cavity trees ≥28 cm dbh.
6. Hardwood, mixed forest, open water, and wetlands mapped by NLCD represent extent of potential habitat or corridors to suitable habitat for ducks as well as current and near future configuration of the landscape.
7. Fuzzed and swapped FIA plot locations were adequate to make Bailey's Ecoregion section-level estimates of suitable nest-cavity abundance.
8. Literature-obtained characteristics of cavities used by cavity-nesting ducks accurately depict suitable cavities, and NLCD water and wetlands coverage represents suitable brood-rearing habitat or corridors to suitable brood-rearing habitat.

RESULTS

The number of FIA plots sampled in the region was 18,965 in 2008, 20,931 in 2018, and 21,875 in 2028. The number increased at each time interval because plots lacking hardwood trees ≥28 cm dbh at earlier simulation stages later contained trees which had grown into cavity-producing size classes. The number of plots within each section varied depending on section area. Total area of hardwood forests as well as total area of hardwood forests located within a given distance of wetlands and open water varied by section (Fig. 2). Over the entire region, 61%, 79%, 88%, and 93% of hardwood forests were ≤0.5 km, ≤1 km, ≤1.5 km, and ≤2 km of water, respectively (Fig. 2). Sections in northern Wisconsin, northern Michigan, and central to northeastern Minnesota had the highest coverage of hardwood forest within close proximity to water (Fig. 2). The southern

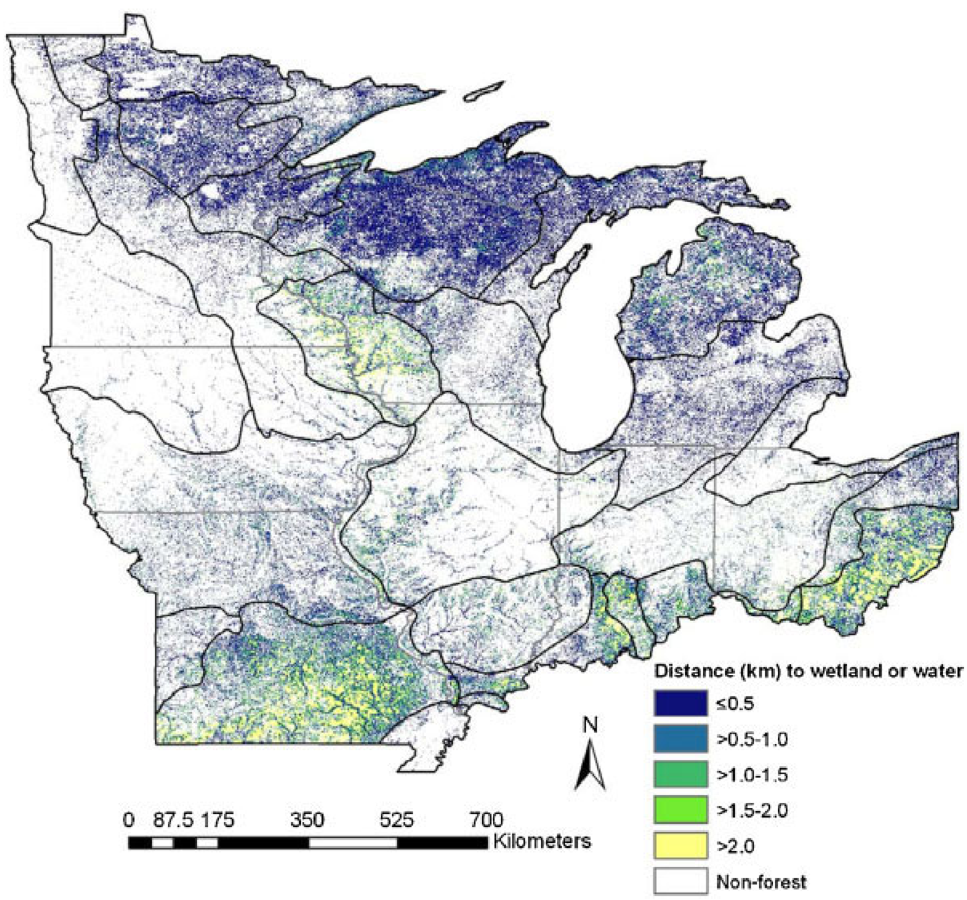

Figure 2. Estimated coverage of hardwood and mixed forests ≤0.5 km, 0.5–1 km, 1.0–1.5 km, 1.5–2.0 km, and >2.0 km of wetland and open water by Bailey's Ecoregion sections, north central United States, 2008.

half of Missouri, southwestern Wisconsin, and the Ohio River Valley of Illinois, Indiana, and Ohio had relatively higher coverage of hardwood forests >2 km from water (Fig. 2). There was less hardwood coverage throughout the central, agriculture-dominated sections of the region (Iowa, Illinois, the northern half of Indiana, western half of Ohio, and southeastern corner of Missouri), but where forests occurred, they were most often in close proximity (<0.5 km) to water (Fig. 2).

Cavity density in all hardwood forests and those in close proximity to water increased in every section between 2008–2018 ($t_{26} = 6.54$, $P < 0.001$) and 2018–2028 ($t_{26} = 7.86$, $P < 0.001$). For the entire region using all plots combined, average potential nest cavities in hardwoods were projected to increase from 0.66 cavities/ha in 2008 to 0.82 cavities/ha in 2018 and to 0.93 cavities/ha in 2028. In 2008, sections of the region with relatively high nest-cavity densities in hardwood forests were found in southeastern Missouri, southern Illinois, northern Wisconsin, and most of Indiana, Ohio, and Michigan (Fig. 3). Only sections of extreme northern Minnesota dominated by coniferous forests had low predicted cavity densities in hardwoods. At each time interval, nest cavities/ha increased until most of the region had relatively high densities in hardwood forests except for northern Minnesota (Fig. 3). We estimated 13.2 million, 17.0 million, 19.0 million, and 20.1 million potential nest cavities available <0.5 km, <1 km, <1.5 km, and <2 km of water, respectively, within the region (Fig. 4). Using predicted changes in suitable nest-cavity density for the entire region, we estimated cavity abundance for cavity-nesting ducks would increase 41% from 2008 to 2028, with the largest increase in cavity production between 2018 and 2028 in the absence of harvest (Fig. 4).

Prevalent tree species for cavity production in the region remained relatively consistent from 2008 to 2028. Sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and American basswood (*Tilia americana*) accounted for 55–60% of nest cavities during the 20-year period (Table 2). By 2018, red maple was predicted to be the second most prevalent test-cavity producer, following sugar maple and overtaking American beech. By 2028, sugar maple and red maple in combination were predicted to produce 42% of the suitable nest sites for cavity-nesting ducks in the region. Currently, the highest proportion of suitable nest cavities for ducks occurs in trees 28–39 cm dbh (Table 3). By 2018, the most important size class for potential nest cavities will be 40–49 cm dbh.

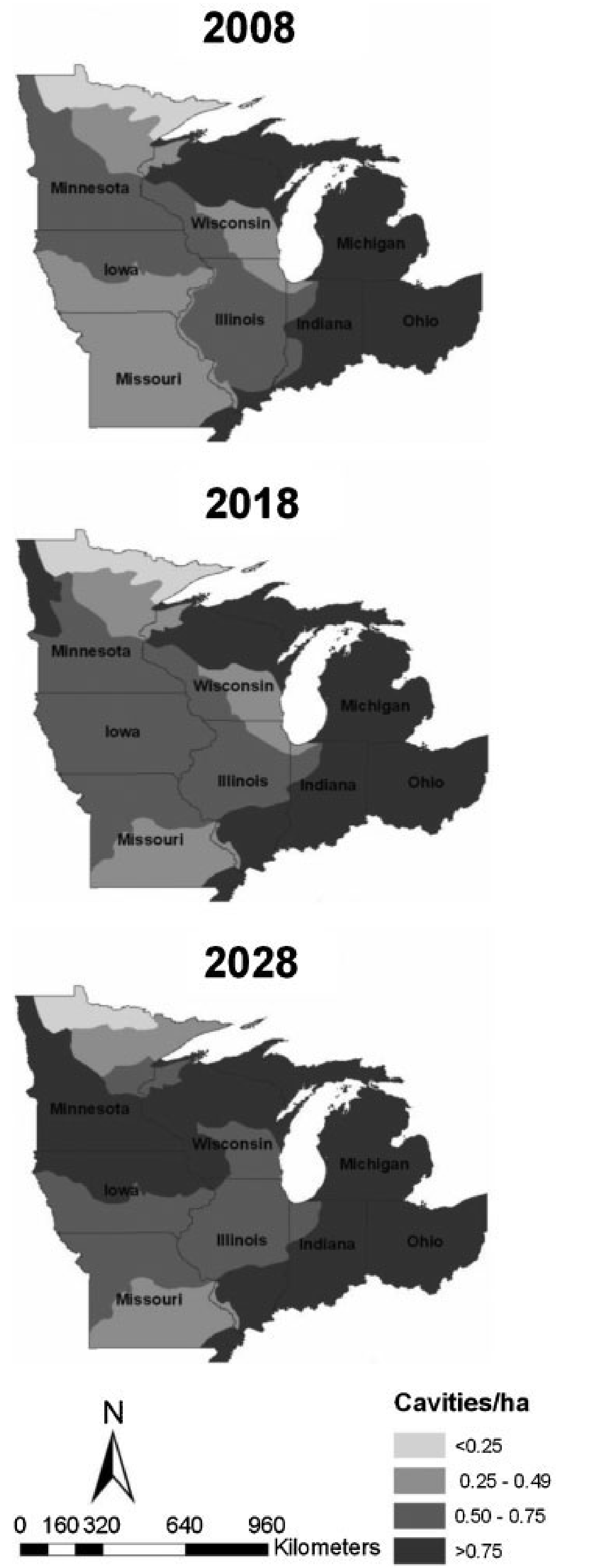

Figure 3. Current estimated and projected suitable nest cavities/ha within all hardwood and mixed forest by Bailey's Ecoregion section for cavity-nesting ducks in the north central United States, 2008–2028.

DISCUSSION

This study was the first to estimate current and future potential nest-cavity abundance for ducks at the regional scale. Suitable nest sites for cavity-nesting ducks are currently abundant in the north central region and will increase as forests continue to mature during 2008–2028. The estimated 13.2 million suitable natural cavities occurring in live hardwood trees within 0.5 km of water alone is substantially more than required to meet cavity-nesting duck population objectives identified for the Upper Mississippi River and Great Lakes Joint Venture region (Soulliere et al. 2007) while also providing habitat for other cavity-dwelling wildlife species. A high proportion of suitable cavities actually go unused by ducks or other species during spring (75%; Zwicker 1999).

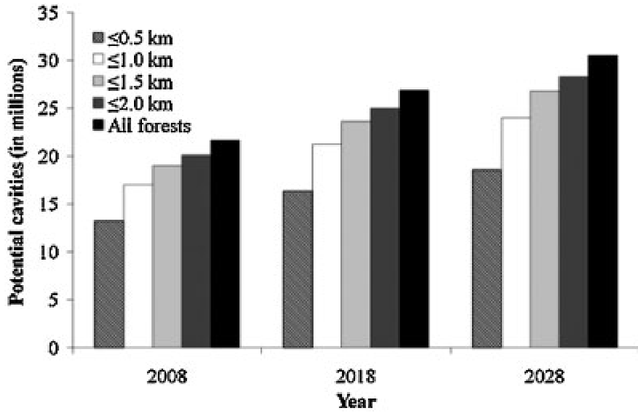

Figure 4. Current and projected number of suitable nest cavities for cavity-nesting ducks in live hardwood trees and ≤0.5 km, ≤1.0 km, ≤1.5 km, and ≤2.0 km of wetlands or open water in the north central United States, 2008–2028.

Moreover, the surplus of nest sites relative to duck population size is substantive considering the conservative nature of our suitable nest-cavity estimates (e.g., cavities in dead trees and conifer-dominated forests were excluded).

Hardwood forests from southeastern Missouri through southern Illinois and covering most of Indiana, Ohio, Michigan, and northern Wisconsin contained high average nest-cavity densities in hardwood forests, and sections in Michigan, Minnesota, and Wisconsin had the highest coverage of hardwood forest in close proximity to water for cavity-nesting ducks (Figs. 2 and 3). Michigan, Wisconsin, and central Minnesota also have the highest densities of breeding cavity-nesting ducks in the region (Soulliere et al. 2007, Sauer et al. 2008). Sections in southern Missouri, southern Illinois, Ohio, and Indiana possess equivalent or higher average nest-cavity densities compared to northern states but much lower breeding duck densities (Soulliere et al. 2007, Sauer et al. 2008). This difference

Table 2. Suitable nest-cavity production by tree species for ducks in the north central United States, 2008–2028.

	Total cavity production (%)		
Species	**2008**	**2018**	**2028**
Acer rubrum	10.0	11.8	15.1
A. saccharinum	2.9	3.5	2.9
A. saccharum	26.4	25.5	27.3
Fagus grandifolia	10.5	9.4	9.5
Quercus alba	2.7	3.1	2.4
Q. lyrata	<0.1	<0.1	<0.1
Q. palustris	0.4	0.5	0.4
Q. phellos	<0.1	<0.1	<0.1
Q. rubra	7.8	7.5	7.2
Liquidambar styraciflua	0.2	0.3	0.3
Sassafras albidum	4.4	4.5	4.5
Liriodendron tulipifera	0.9	0.9	0.9
Nyssa sylvatica	3.8	3.2	2.8
Fraxinus pennsylvanica	1.8	2.0	2.0
Platanus occidentalis	2.8	2.9	2.3
Populus tremuloides	3.1	2.9	2.8
Tilia americana	10.0	8.5	7.6
Ulmus americana	2.1	2.6	2.6
Other species	10.2	10.9	9.4
Total	100	100	100

Table 3. Percentage of suitable nest-cavity production for ducks by tree diameter at breast height (dbh) for the north central United States at 10-year intervals, 2008–2028.

	% Total cavity production		
Dbh (cm)	**2008**	**2018**	**2028**
28–39	38.2	34.6	32.2
40–49	36.9	37.9	37.7
50–59	15.6	17.3	18.7
60–69	5.9	6.4	7.1
70–79	2.0	2.3	2.6
≥80	1.4	1.5	1.7
Total	100	100	100

suggests the importance of protecting, restoring, or maintaining additional wetlands near forests where increasing breeding populations of cavity-nesting ducks is a goal.

Sugar and red maple were the most common cavity trees throughout the simulation period due to their abundance on the landscape and their ability to form suitable nest cavities more often than most other tree species. Our projections indicated American beech and American basswood were less abundant in the region but produced cavities at an even greater rate than maples. The proportion of potential nest cavities contributed by each tree species remained fairly stable throughout the simulation, although the proportion contributed by a few species declined slightly due in most part to an increasing contribution of cavities by red maple. An increase in red maple abundance has been documented throughout its range (Abrams 1998) and was evident at each time interval during the simulation. Red maples are generalists with high tolerances to various climates, soil conditions, and amounts of sunlight (Burns and Honkala 1990, Abrams 1998), allowing them to flourish under most conditions. In addition, other stochastic processes (e.g., forest succession) which are incorporated into the FVS model also contributed to fluctuations in the relative importance of species to suitable cavity production at different time intervals. Sugar maple and red maple will be the most important species regionally for future nest cavity production due in part to their wide distribution. Although nest-cavity densities will continue to increase in forests containing American beech and sycamore (*Platanus occidentalis*), the relative importance of these species will decline at the regional scale because they are not prevalent in northern portions of the region.

Tree abundance was more important than per capita cavity production when comparing cavity production across dbh size classes. Though rates of nest-cavity production were relatively low, the more numerous 28–39 cm dbh trees were the most important contributing size class in 2008. Larger trees (≥40 cm) produced more cavities relative to their abundance and became increasingly prevalent throughout the simulation period.

Our modeling effort had limitations, which tended to make our estimates conservative. First, we excluded cavities in dead trees when calculating nest-site abundance because standing dead timber could not be discriminated from downed trees during FVS simulations (i.e., standing dead timber may provide suitable nest sites whereas downed dead timber will not). We found 16% of suitable cavities in dead trees at the 4 study sites (Denton 2009), thus standing dead trees not accounted for in simulations contribute to greater nest-cavity abundance. Second, our suitable nest cavity/tree estimates were likely conservative because we could not assess several cavity entrances that we identified in trees unsafe to climb (Denton 2009). In combination, these 2 factors may represent a significant number of suitable cavities unaccounted for in our analysis.

Several of our assumptions, if untrue, could potentially bias our estimates of nest-cavity abundance. First, cavity-tree measurements occurred on lands with various historical, geomorphic, and hydrologic conditions. We argue that our use of species-specific values, rather than stand-specific values for cavity estimates permitted the implicit incorporation of many of these factors. Because each species is adapted to a suite of habitat conditions that are tied to these conditions, areas with differing history, geomorphology, and hydrology will contain different assemblages of species. We handled each tree as a member of a species and size class rather than as the member of a forest stand in determining its probability of possessing a cavity. Furthermore, although cavity formation is a stochastic process (Fan et al. 2003, 2004*a*, *b*) which can vary among otherwise similar stands, it is positively correlated with increasing individual tree size regardless of overall stand attributes (e.g., tree density, species composition; Goodburn and Lorimer 1998, Fan et al. 2003). Therefore, using an individual-tree rather than stand-level approach to sampling and modeling of cavity density in the region should reduce biases associated with sample tree location.

Similarly, the majority of cavity-tree measurements occurred on public lands with little to no harvest. Harvest is a source of disturbance that may directly (e.g., logging damage) or indirectly (e.g., increased wind damage) increase injury to trees. However, the lack of inclusion of these trees that are probably more prone to injury only served to make our cavity estimates more conservative.

The 2008 estimates included forest conditions as they were during the latest forest inventory (i.e., with and without timber harvest), but timber harvest could not be simulated in future conditions because of difficulty gathering information on harvest plans that varied locally and temporally. However, annual volume growth has exceeded average annual volume harvest since 1953, and in 2006, there was twice as much volume growth of hardwoods compared to volume harvest of hardwoods in the region (0.08 billion m^3 and 0.04 billion m^3, respectively; FIA 2007). This trend is expected to persist in the region (Shifley and Sullivan 2002). In addition, the effect of timber harvest to future cavity production will likely be small considering the magnitude of differences between estimated potential suitable cavities and duck populations in the region.

We assumed only trees $\geq$28 cm dbh are large enough to house a cavity suitable for duck nesting. Cavities suitable for duck nesting have occurred in enlarged areas of trees <28 cm dbh (Denton 2009), but we argue this extremely rare contribution would not significantly increase cavity abundance. Similarly, conifers and conifer-dominated forests were not included in simulations, because conifers produce a relatively small number of nest cavities (C. Gayle, unpublished report; Bellrose and Holm 1994, Vaillancourt et al. 2009) and we focused our cavity-measurements on hardwoods. The model did not include the contribution of growth of new trees from seedlings (<2.5 cm) into the simulation, but few trees are capable of growing to $\geq$28 cm dbh in just 20 years in the study region (Burns and Honkala 1990).

We assumed current distribution of cover types identified by the NLCD represented the current and future configuration of the landscape because we had no other consistent spatial data (or trend data) at the regional scale. Modifications to this configuration could influence the availability of forests near water. Additionally, we assumed fuzzed and swapped FIA plot locations were adequate to make section-level estimates of suitable nest-cavity abundance. We chose large areas of interest (Bailey's Ecoregion sections) to nullify the impacts that fuzzed and swapped plot locations would have at a finer scale since estimates derived from fuzzed and swapped plots are highly correlated with estimates derived from plots using actual locations when areas of interest are large ($\geq$20-km radii [125,664 ha]; Lister et al. 2005, McRoberts et al. 2005). All Ecoregion sections were $\geq$153,535 ha, and the majority of sections were much larger. Furthermore, mean cavity density/section was calculated using all plots within a section regardless of distance from water and then multiplied by the total area of hardwood forests/section and by the area of hardwood forests within $\leq$0.5 km, >0.5–1 km, >1–1.5 km, >1.5–2 km, and >2 km/section, so plot location should have no impact on our large-scale abundance estimates. Future research that incorporates actual locations of FIA plots would provide additional insights at a finer scale.

Finally, we assumed suitability criteria based on actual cavity-nesting duck nests from the literature accurately depict suitable cavities for cavity-nesting ducks. This was the most current data available on cavity nests used by ducks. These studies may not capture some cavities that would be deemed suitable by ducks, or include cavities that would rarely be considered suitable by a duck. Similarly, we assumed open water and wetland NLCD codes were available as brood-rearing habitat or corridors to brood-rearing habitat for cavity-nesting ducks. This assumption was necessary due to the lack of concurrence in defining brood-rearing habitat requirements for each species and the generality of NLCD mapping, which did not allow mapping of specific brood-rearing habitat. Additionally, upon exit from the nest, individual cavity-nesting ducks have led broods up to 15 km along rivers to reach primary brood-rearing areas while bypassing seemingly suitable brood-rearing wetlands as well as sites being used by other broods (Granfors and Flake 1999).

Populations of the 3 cavity-nesting duck species common to the region are believed to be stable or increasing throughout their respective ranges (Sauer et al. 2008), and the number of hardwood trees large enough to produce suitable nest cavities for ducks is higher now than it has been in over a century (FIA 2007). Our estimates of cavity abundance confirm more than adequate nest sites to support growing duck populations in the north central region. Millions of suitable tree cavities currently available to nesting ducks in the region are predicted to increase by another 41% by 2028. Similar increases (44% by 2038) were predicted by Roy Nielsen et al. (2007) using a slightly different method for 2 hardwood forests in southern Illinois. Regional population growth of cavity-nesting ducks will not likely surpass nest-cavity abundance, unless dramatic changes in timber harvest occur. If timber harvest rates remain similar to current levels, as they are expected to (Shifley and Sullivan 2002), cavities suitable for cavity-nesting ducks will increase over the next 20 years.

MANAGEMENT IMPLICATIONS

Wildlife habitat management decisions are made at the local scale, thus appropriate use of this regional information might include supplements of site-specific data regarding nest-site abundance. Nevertheless, our results indicate nest sites are not limiting cavity-nesting ducks at a regional scale. Given that all 8 states in the region lost >40% of their wetlands between the 1780s and 1980s (Illinois, Indiana, Iowa, and Missouri lost >85%; Dahl 1990), restoration of aquatic systems providing value to breeding ducks will be a more effective use of conservation resources compared to supplementing nest site abundance. Waterfowl managers may target wetland conservation efforts to take advantage of the high duck nest cavity densities in sections of northern Wisconsin, central and eastern Minnesota, Missouri, southern portions of Illinois, and large portions of Indiana, Michigan, and Ohio with dominant hardwood coverage. This is especially true for wetland restoration in Illinois, Indiana, and Ohio, where our forest-cavity mapping reveals abundant potential duck nest sites but at greater distance from water and wetlands.

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