



Birds see the trees inside the forest: The potential impacts of changes in forest composition on songbirds during spring migration

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ABSTRACT

Since European settlement, hardwood dominated forests of the Upper American Midwest have undergone compositional changes due to fire suppression and changes in land use. It is not clear how these changes affect songbirds during spring migration. In 2009 and 2010, we quantified foraging behavior by migratory songbirds during spring migration and collected data on tree and sapling diversity in the Kickapoo Valley Reserve in southwestern Wisconsin. Furthermore, we compared the 1840s distribution of tree species (from Public Land Survey System witness tree records) with current (2010) and estimated future (sapling) tree-composition to better understand how historic and future changes in tree composition may impact migratory songbirds at spring migration stopover sites. Six tree species were selected as foraging substrates in higher proportion than they were available by eight migratory songbirds, including trees adapted to moderate shade such as northern red oak (*Quercus rubra*), white oak (*Quercus alba*), American elm (*Ulmus americana*), and slippery elm (*Ulmus rubra*), and shade-intolerant species such as big-tooth aspen (*Populus grandidentata*), and paper birch (*Betula papyrifera*). Whereas three shade-tolerant tree species were selected in far lower proportion than they were available by eight migratory songbirds, including sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and basswood (*Tilia americana*). We found evidence that food accessibility, as measured by a novel approach relating a bird's attacks and search efforts to the average leaf petiole length of a tree species, was strongly inversely related with a bird's foraging success ($\rho = -0.96$, p -value < 0.001). Although tree-species composition changed considerably from the 1840s to 2010, in both time periods the forest was dominated by a mix of sugar maple and oak species. However, sugar maple saplings currently form a nearly continuous layer in the understory and there is very low recruitment of shade-intolerant or moderately shade-tolerant species, suggesting a future shift towards dominance by shade-tolerant species. Our results suggest the current trajectory of forest succession may result in future conditions that provide lower quality foraging for migratory songbirds during spring migration than they currently experience in the Upper American Midwest.

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1. Introduction

Spring migration is a taxing time in the life cycle of migratory songbirds (Hutto, 2000; Sillett and Holmes, 2002; Newton, 2004, 2006; Hedenström, 2008). Among the many challenges birds face, such as predators, (Lindström, 1990; Schmaljohann and Dierschke, 2005; Lind and Cresswell, 2006), exhaustion (Yong et al., 1998), inhospitable weather (Rappole and Warner, 1976; Richardson, 1978), and inter- and intra-specific competition (Moore and Yong, 1991), birds must make critical decisions regarding resource selection at stopover habitats (Moore et al., 2005; Chernetsov, 2006; Buler et al., 2007; Smith et al., 2007; Rodewald and Brittingham, 2007). Using optimal stopover habitat allows birds to refuel efficiently and thus to depart as quickly as possible to the next stop-

over location or breeding area (Loria and Moore, 1990; Moore and Yong, 1991; Moore and Simons, 1992; Moore et al., 1995; Smith and Moore, 2003; Schaub et al., 2008). Birds that arrive in breeding habitat earliest maximize opportunities to produce offspring that survive (Norris et al., 2004). Therefore, since migration requires substantial energy, the ability to discern which foraging substrates maximize energy intake at stopover habitats is likely a trait that has undergone strong selection pressure, due to the effect on fitness and survival of all migratory species (Berthold and Ter- rill, 1991; Moore et al., 2005).

In the Upper American Midwest, human land use has altered the structure and composition of hardwood dominated forests (Rhemtulla et al., 2007, 2009). During the 19th century, large areas of forest were cleared for timber extraction, agricultural development, and Euro-American settlement (Schulte et al., 2007; Rhemtulla et al., 2009). Yet, over the last approximate half century, forest cover has increased throughout the region primarily

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because of shifts in land use practices (Iverson et al., 1997; McShea et al., 2007; Rhemtulla et al., 2007). In southwestern Wisconsin, successional trends are characterized by the term ‘mesophication’ (Lorimer, 1984, 1985; Abrams, 1992, 2005; Nowacki and Abrams, 2008). This term embodies the process, due in large part to widespread fire suppression, of the decline of fire adapted tree species. As a result, oak (*Quercus* spp.) and other tree species that require canopy openings for seedling germination and sapling maturation have declined in importance, while shade-tolerant species like maple (*Acer* spp.) have increased (Hix and Lorimer, 1991; Lorimer et al., 1994; Taylor and Lorimer, 2003; Rogers et al., 2008). In southern Wisconsin, oak-hickory, which was the most common deciduous habitat in the mid-1800s, has declined by 47%, while northern hardwoods habitat (e.g., maple) has increased by 58% (Rhemtulla et al., 2009).

Oaks are regarded as keystone species for their value in maintaining biodiversity in North American forests (Fralish, 2004; McShea et al., 2007). Many breeding birds and some mammal species are more common in oak dominated than maple dominated forests, due to greater resource availability (e.g., acorn mast, arthropods, and cavities, Rodewald and Abrams, 2002; Rodewald, 2003; McShea et al., 2007). Moreover, oaks support higher Lepidopteran richness than other tree species (Tallamy and Shropshire, 2009), an important foraging resource for migratory songbirds (Graber and Graber, 1983).

Yet the effect of changes in forest tree composition on migratory songbirds at habitats encountered during spring migration is unclear. Many canopy foraging insectivorous migratory songbirds are in decline (Robbins et al., 1989), and it has been suggested that mortality may be highest during the migratory period (Sillert and Holmes, 2002). Quantifying tree preferences by foraging migratory songbirds is an important step in understanding the implications of broad scale tree-compositional changes on the spring migratory songbird community in Upper American Midwest forests.

In this study we had three objectives. First, in order to explore how changes in tree composition may impact a subset of the migratory songbird community, we investigated tree species preferences by eight migratory songbirds for fifteen tree species that were either common in 2010 or the 1840s. Also, to better understand individual migratory songbird tree preference and aversion patterns, we examined tree species preferences by eight migratory songbirds for eleven tree species that were either common or frequently used as foraging substrates. We expected birds to display plasticity in their preference of trees as they do during the breeding season (Holmes and Robinson, 1981; Gabbe et al., 2002) and spring migration in other locations (Graber and Graber, 1983; Strode, 2004, 2009). Our second objective was to determine whether food accessibility was related to selection of tree species as foraging substrates by migratory songbirds. We predicted that migratory songbirds would have higher foraging success on tree species with shorter petiole length than longer petiole length, likely because of greater ease of procuring prey items, a hypothesis first put forth by Holmes and Robinson (1981). We applied a novel approach to quantify the importance of this leaf characteristic, relating a bird's attacks and search efforts to the average leaf petiole length according to tree species. Our third objective was to examine changes in tree species composition over time and how this may affect availability of suitable stopover sites for migratory songbirds.

2. Materials and methods

2.1. Study site

Our study site was the 3468 ha Kickapoo Valley Reserve in southwestern Wisconsin, located in the Driftless Area, an unglaci-

ated area of greater topographical heterogeneity than the surrounding landscape (Curtis, 1959, Fig. 1). The Driftless Area is an important stopover region for migratory songbirds *en route* to breeding habitat in the boreal forest (Wilson, 2008). The vegetation of the Kickapoo Valley Reserve ranges from bottomland hardwood forest in the Kickapoo River floodplain to upland dry- and southern-mesic forest on the surrounding ridges (Curtis, 1959). This study was conducted in the upland dry- and southern-mesic forests which included 32 tree species (Table 1).

Field work was conducted in four sites which represent some of the largest tracts of contiguous forest in the Driftless Area of Wisconsin (ranging from 80 to 107 ha, Fig. 1). In addition to being large and unfragmented, these sites were selected for their diverse tree composition (> than 20 tree species per site) and because they are compositionally representative of smaller forest sites within the Driftless Area. Using a high-resolution air photo, we digitized each site in ArcGIS 9.1 (ESRI, Redlands, California, USA, 2006) and plotted a lattice grid of points (hereafter lattice points) separated by 100 meters, with alternate rows offset by 50 meters. Each lattice point was used as a sampling location where we determined tree and sapling composition and as a reference point for walking routes established for avian observations. Eighty-three, 52, 61, and 62 lattice points were plotted in the four sites for a total of 258 lattice points (Fig. 1).

2.2. Avian foraging observations

To determine which tree species migratory songbirds prefer during spring migration we collected foraging data from early-April to early June in 2009 and 2010, which encompasses the migration period in Wisconsin for the majority of migratory songbirds *en route* to northern breeding grounds (Temple et al., 1997). Between sunrise and 1 pm, an observer proceeded along a walking route established to maximize coverage of a forest site, and actively searched for foraging flocks of eight migratory songbird species (hereafter focal species, Table 2) using standardized methods (Holmes and Robinson, 1981; Remsen and Robinson, 1990). Focal species were chosen because they are relatively common migratory songbirds that primarily use trees as foraging substrates during spring migration in our study area. Blue-gray Gnatcatcher (*Poliophtila caerulea*) was not a focal species in 2009 but was included in 2010. Since the average length of stay of migratory songbirds at stopover sites is less than three days (Moore and Kerlinger, 1987), we visited the four sites on average twice a week during the sampling periods, with at least three days separating visits to reduce the risk of autocorrelated foraging observations. The starting point of the walking routes alternated so unique sections of each forest site were visited at similar times (e.g., early morning) among visits. Four trained observers, including the lead author, collected data each year and rotated among forest sites with each visit in an effort to distribute observer variability as much as possible.

Once an individual of a focal species was detected, an observer followed and documented the individual's activities and movements for as long as possible up to 5 min and within the boundaries of a forest site. Although we often followed and documented foraging behavior of focal birds in multiple trees during a foraging observation, for comparisons of tree use versus availability, we restricted our definition of ‘use’ to the first tree in which a focal bird was observed actively attacking a prey item (Holmes and Robinson, 1981; Gabbe et al., 2002). However, foraging data from an individual bird foraging on multiple trees was used for other analyses. Using a digital recorder with a built in timer (Sony ICD-PX720 Digital Voice Recorder) the observer documented the following data for each individual: date, time, species, sex (if possible), tree species used, search effort (e.g. number of hops, walks, flights), and type of attack (e.g., bud glean, flower glean, leaf glean,

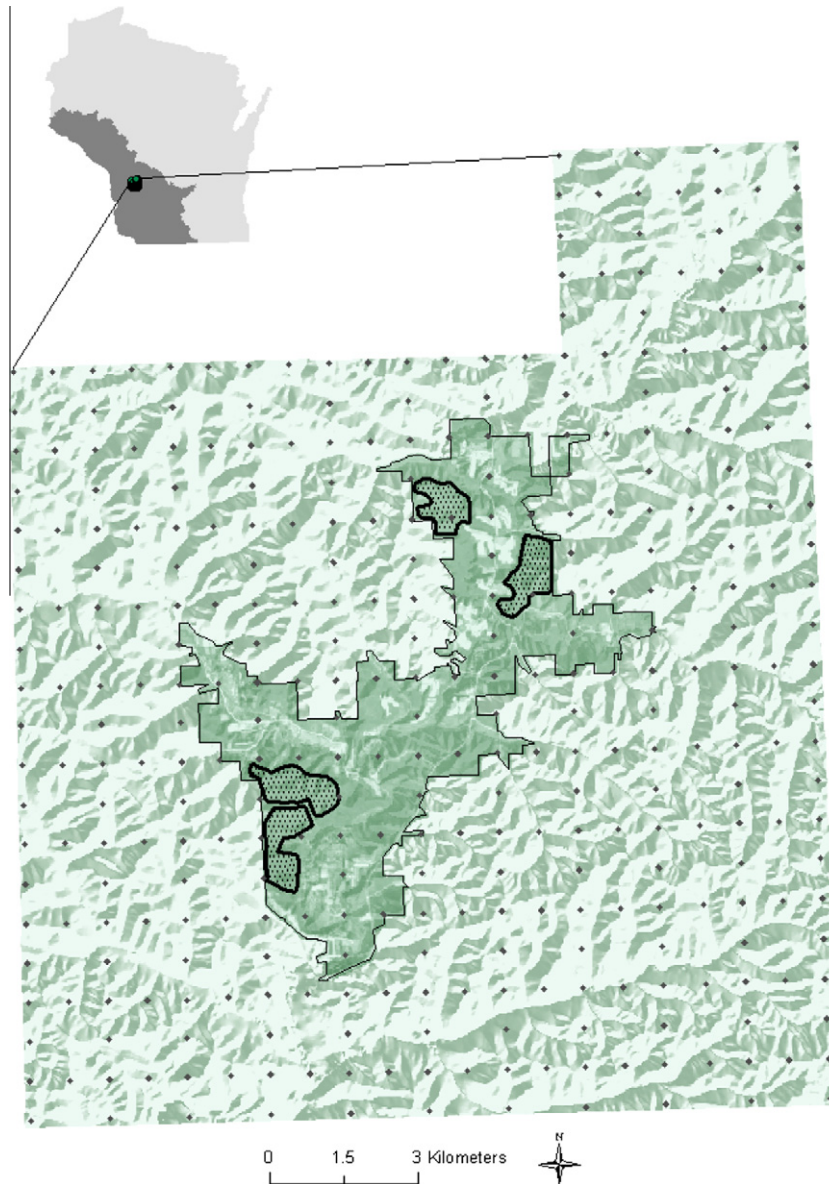


Fig. 1. Location of Kickapoo Valley Reserve (in dark green), within the Driftless Area (darker gray), Wisconsin, USA. Black outlined polygons indicate the locations of forested sites where current tree and sapling data were collected at 258 lattice points that are superimposed on these plots. Foraging observations were collected in the boundaries of these four sites. The larger surrounding point-grid (light green) is 326 corner and mid-section Public Land Survey System locations used to estimate 1840s historic forest composition profile of the Kickapoo Valley Region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

bark glean, hover, sally, and flush-chase, Remsen and Robinson, 1990). In order to accurately quantify location of bird attacks (e.g., bud glean), it was necessary for the field crews to be familiar with tree phenology. For a parallel study, we collected information on tree phenology and field observers were extensively trained by the lead author in quantifying tree phenophases (e.g., flowering, mature leaf, Richardson et al., 2006).

Once a data collection session for an individual of a focal species was concluded, the observer either moved to another individual of a focal species in the immediate area, if possible, or moved back to the walking route in search of another foraging flock, moving at least 300 m from the previous flock before beginning a new data collection session. To guard against inadvertently collecting foraging data twice on the same individual, only one male or female of a dichromatic species [e.g., Black-throated Green Warbler (*Setophaga virens*)] in a flock was counted. Thus, if multiple male Black-throated Green Warblers were detected in a flock, foraging data was only collected on the first male encountered. The observer

then proceeded to collect foraging information on a female, or a different species, if detected. For focal species that are weakly sexually dichromatic, such as a Tennessee Warbler (*Oreothlypis peregrina*), foraging data was collected on only one individual within a flock. The Blue-gray Gnatcatcher, Blue-winged Warbler (*Vermivora cyanoptera*), and Chestnut-sided Warbler (*Setophaga pensylvanica*) are migratory songbirds that breed in our study area (Wisconsin Breeding Bird Atlas, 2011). Thus, we only collected foraging observations on individuals of these three species that were actively moving in a mixed-species foraging flock composed mainly of focal species migrating to more northerly breeding grounds [e.g., Blackburnian Warbler (*Setophaga fusca*) and Black-throated Green Warbler].

2.3. Leaf petiole measurements

We predicted that the length of the leaf petiole influences access to invertebrate prey, a hypothesis first put forth by Holmes

Table 1

Thirty-two tree species, grouped by shade tolerance, studied at the Kickapoo Valley Reserve, southwestern Wisconsin. Frequency, density, and dominance measurements collected using the point center quarter method from which importance values (importance) were calculated. Cell numbers are relative values.

| Tree species | Scientific name | Frequency | Density | Dominance | Importance |
|-------------------------------------|-------------------------------|-----------|---------|-----------|------------|
| <i>Shade intolerant</i> | | | | | |
| Paper birch | <i>Betula papyrifera</i> | 1.36 | 1.17 | 0.48 | 1.00 |
| Butternut | <i>Juglans cinerea</i> | 0.14 | 0.10 | 0.23 | 0.16 |
| Eastern black walnut | <i>Juglans nigra</i> | 0.27 | 0.19 | 0.45 | 0.31 |
| Eastern red-cedar | <i>Juniperus virginiana</i> | 0.41 | 0.39 | 0.09 | 0.30 |
| Tamarack | <i>Larix laricina</i> | 0.27 | 0.68 | 0.50 | 0.48 |
| Balsam poplar | <i>Populus balsamifera</i> | 0.14 | 0.10 | 0.21 | 0.15 |
| Big-tooth aspen | <i>Populus grandidentata</i> | 2.18 | 2.53 | 2.98 | 2.56 |
| Quaking aspen | <i>Populus tremuloides</i> | 0.95 | 0.97 | 0.79 | 0.90 |
| Black cherry | <i>Prunus serotina</i> | 2.99 | 2.63 | 1.51 | 2.38 |
| Black willow | <i>Salix nigra</i> | 0.14 | 0.10 | 0.54 | 0.26 |
| <i>Intermediate shade tolerance</i> | | | | | |
| Yellow birch | <i>Betula alleghaniensis</i> | 0.82 | 0.88 | 0.65 | 0.78 |
| Bitternut hickory | <i>Carya cordiformis</i> | 9.66 | 9.73 | 4.58 | 7.99 |
| Shagbark hickory | <i>Carya ovata</i> | 0.82 | 0.58 | 0.43 | 0.61 |
| Common hackberry | <i>Celtis occidentalis</i> | 0.41 | 0.29 | 0.19 | 0.30 |
| Hawthorn | <i>Crataegus</i> spp. | 0.27 | 0.19 | 0.04 | 0.17 |
| White ash | <i>Fraxinus americana</i> | 3.95 | 3.21 | 2.63 | 3.26 |
| Black ash | <i>Fraxinus nigra</i> | 0.41 | 0.29 | 0.16 | 0.29 |
| Green ash | <i>Fraxinus pennsylvanica</i> | 0.14 | 0.10 | 0.10 | 0.11 |
| Eastern white pine | <i>Pinus strobus</i> | 2.18 | 1.85 | 3.86 | 2.63 |
| White oak | <i>Quercus alba</i> | 12.93 | 15.18 | 20.34 | 16.15 |
| Bur oak | <i>Quercus macrocarpa</i> | 2.72 | 2.14 | 2.48 | 2.45 |
| Northern red oak | <i>Quercus rubra</i> | 11.16 | 10.80 | 28.18 | 16.71 |
| Eastern black oak | <i>Quercus velutina</i> | 2.04 | 1.95 | 2.43 | 2.14 |
| American elm | <i>Ulmus americana</i> | 4.90 | 4.57 | 1.66 | 3.71 |
| Slippery elm | <i>Ulmus rubra</i> | 2.99 | 2.53 | 1.14 | 2.22 |
| <i>Shade tolerant</i> | | | | | |
| Box elder | <i>Acer negundo</i> | 0.54 | 0.39 | 0.14 | 0.36 |
| Red maple | <i>Acer rubrum</i> | 5.85 | 5.84 | 3.84 | 5.18 |
| Sugar maple | <i>Acer saccharum</i> | 16.73 | 19.07 | 11.06 | 15.62 |
| American hornbeam | <i>Carpinus caroliniana</i> | 0.14 | 0.10 | 0.06 | 0.10 |
| American hophornbeam | <i>Ostrya virginiana</i> | 4.49 | 4.18 | 0.79 | 3.16 |
| Basswood | <i>Tilia americana</i> | 7.89 | 7.10 | 7.30 | 7.43 |
| Eastern hemlock | <i>Tsuga canadensis</i> | 0.14 | 0.19 | 0.18 | 0.17 |

Table 2

Eight migratory songbird species studied, including the number of foraging observations (*n*) and cumulative number of seconds, displayed in superscript, each species was observed foraging during the 2009 and 2010 spring migration in the Kickapoo Valley Reserve, southwestern Wisconsin.

| Migratory songbird species | Alpha code | Scientific name | <i>n</i> 2009 | <i>n</i> 2010 | <i>n</i> 2009–2010 |
|-------------------------------------|------------|------------------------------------|--------------------|--------------------|----------------------|
| Blue-gray gnatcatcher ^a | BGGN | <i>Poliptila caerulea</i> | 2 ¹⁶⁵ | 21 ¹²⁸⁸ | 23 ¹⁴⁵³ |
| Blue-winged warbler ^a | BWWA | <i>Vermivora cyanoptera</i> | 19 ²¹⁴⁸ | 10 ⁶⁶⁶ | 29 ²⁸¹⁴ |
| Tennessee warbler | TEWA | <i>Oreothlypis peregrina</i> | 70 ⁷²¹⁹ | 35 ³⁶⁰⁴ | 105 ¹⁰⁸²³ |
| Nashville warbler | NAWA | <i>Oreothlypis ruficapilla</i> | 16 ²²⁸⁹ | 18 ¹⁵⁹² | 34 ³⁸⁸¹ |
| Blackburnian warbler | BLBW | <i>Setophaga fusca</i> | 20 ²⁷⁴² | 7 ⁷³⁴ | 27 ³⁴⁷⁶ |
| Chestnut-sided warbler ^a | CSWA | <i>Setophaga pensylvanica</i> | 11 ⁸³⁰ | 5 ⁴¹⁴ | 16 ¹²⁴⁴ |
| Black-throated green warbler | BTNW | <i>Setophaga virens</i> | 19 ³⁵¹⁸ | 16 ¹³⁸⁵ | 35 ⁴⁹⁰³ |
| Myrtle yellow-rumped warbler | MYWA | <i>Setophaga coronata coronata</i> | 19 ²⁸⁰⁰ | 15 ¹⁰⁰¹ | 34 ³⁸⁰¹ |

^a Species breeds in study area (Wisconsin Breeding Bird Atlas, 2011).

and Robinson (1981), and further tested by Whelan (2001), but not considered outside of the breeding period in New Hampshire. Migrating birds have higher energy expenditure on average than breeding birds (Moore et al., 1995, 2005) and thus may apply different foraging strategies to maximize energy intake while minimizing energy output. We characterized data on leaf petiole length by measuring leaf specimens housed in the University of Wisconsin Herbarium that were obtained by branch clipping from trees, not saplings, within 35 km of the Kickapoo Valley Reserve. We measured leaf petiole length from University of Wisconsin-Madison Herbarium samples rather than in the field because many of the tree crowns in our study sites were tall (> 25 m) and it was logistically difficult to obtain leaf samples from these trees. We measured leaf petiole specimens that had been collected approximately over the past half century, in mid-May to early June to match the period when focal bird species use Driftless Area forests

during migration (Temple et al., 1997). The leaf samples were obtained either from fallen branches, branch clippings, or felled trees. A small proportion of leaf petiole specimens were not mature (i.e., not in summer condition). However, we measured all growing and mature leaf petiole specimens for a tree species because this depicted the variable conditions (i.e., spring tree phenology) migratory songbirds encounter during spring migration and we commonly observed focal species foraging on both growing and mature leaf surfaces among trees. Tree species were selected for this analysis because they were frequently used as foraging substrates by migratory songbirds, were commonly encountered in our study, and there were adequately preserved (i.e., pressed) and available leaf specimens for measurements at the Herbarium. The eleven tree species included basswood (*Tilia americana*, *n* = 62 leaf petiole measurements), American (*Ulmus americana*, *n* = 95) and slippery elm (*Ulmus rubra*, *n* = 63), big-tooth aspen

(*Populus grandidentata*, $n = 71$), bitternut hickory (*Carya cordifor-
mis*, $n = 28$), paper birch (*Betula papyrifera* $n = 81$), northern red
(*Quercus rubra* $n = 105$) and white oak (*Quercus alba* $n = 105$), red
(*Acer rubrum*, $n = 31$) and sugar maple (*Acer saccharum*, $n = 27$),
and white ash (*Fraxinus americana*, $n = 102$). For each tree species,
the leaf petiole measurements were averaged and this metric was
used for further analysis. Two tree species, white ash and bitternut
hickory, have compound leaves composed of individual leaflets.
Focal species were often observed perched on the rachis of the
white ash gleaning prey items from individual leaflets. Therefore,
we measured the length of each white ash leaflet petiole. Focal spe-
cies were not observed using the rachis of the bitternut hickory but
were observed foraging on leaves while perched on a branch. For
this species we used the distance from the branch to the first leaflet
pair as a measure of food accessibility.

2.4. Tree and sapling availability

To gain information on the current tree composition at each of
the 258 lattice points, we used the point-center quarter method
(Cottam and Curtis, 1956; Curtis, 1959; Mitchell, 2001). We re-
corded tree species, measured diameter-at-breast height (dbh),
and distance from lattice point of the closest tree (>10 cm dbh)
in each of four quadrants: 0–90°, 90–180°, 180–270°, and 270–
360°. We calculated the importance value, of all tree species as fol-
lows: importance value = relative frequency + relative density +
relative dominance (Cottam and Curtis, 1956; Curtis, 1959;
Mitchell, 2001). The term 'relative' refers to the proportion, for a gi-
ven tree species, of the total when considering all trees. We used
the relative importance value (i.e., the importance value of each
tree relative to importance of all available trees) to represent the
availability of each tree species as foraging substrate (Holmes
and Robinson, 1981). As an estimate of the potential future forest
tree composition, we again used the point-center quarter method,
recording species and distance to the closest tree sapling (<10 cm
dbh and taller than 1.3 m) in each quadrant. We calculated relative
density of saplings, by species, for comparison with historic and
current tree data.

2.5. Public Land Survey System data

To determine historic tree composition of the Kickapoo Valley
Region, we used Public Land Survey System data (Schulte and
Mladenoff, 2001; Liu et al., 2011). The Public Land Survey System
(PLSS) was implemented by the United States government in
1785 to partition western lands into parcels for settlement in
township (6 × 6 mile; 9.7 km²) and section (1 × 1 mile; 2.6 km²)
increments (Schulte and Mladenoff, 2001). At the midway point
and corner of each section, surveyors recorded the dbh, distance
to, and species of two to four 'witness' trees. The PLSS data were
collected in the 1840s in southwestern Wisconsin.

Because the PLSS data was collected at a coarser resolution than
our current tree data, we needed to increase the sample size of
1840s data for comparability with current data. Therefore we in-
cluded 1840s era corner and mid-section tree data from the Kick-
apoo Valley Reserve plus 23,500 ha of surrounding upland habitat
that is similar in elevation and topography (Fig. 1). From this larger
area, 326 corner and mid-section points and 651 witness trees
were available for analysis. In order to compare compositional
and importance trends in tree species since the 1840s, we calcu-
lated the importance value of each witness tree species.

2.6. Statistical analysis

To determine whether the focal species foraged on trees in pro-
portion to the availability of those tree species, we used a chi-

square goodness-of-fit exact test to compare observed use- versus
expected use-frequencies for all focal species as a group (Holmes
and Robinson, 1981). A Fisher's exact test was used to estimate sig-
nificance because migratory songbird expected use-frequencies
were low for some tree species. To obtain the expected use-fre-
quencies, we multiplied tree importance values (see Tree and sap-
ling availability section for formula) by the total number of
observations of each focal species (Gabbe et al., 2002). Since most
focal species in our study area used only a small proportion of the
available tree species as foraging substrates, we pooled observed-
use data from the eight focal species and compared these with
the pooled expected use-frequencies. Pooling data for this analysis
allowed for an exploration of tree preferences for members of the
migratory songbird community and how potential changes in tree
species composition may impact these bird species. Similar to the
leaf petiole analysis, eleven tree species were used for this analysis.

To quantify tree-species preferences by each focal species, we cal-
culated preference and aversion values (Holmes and Robinson,
1981). Preference and aversion values were the difference of the re-
lative percent use by focal species and the relative importance per-
centage of a given tree species. These values represent a bird's
foraging selectivity with higher values indicating greater preference.

To determine focal species foraging success related to leaf-pet-
iole length, we calculated a 'leaf attack index', which is a novel
method of computing foraging success. The leaf attack index is
the pooled number of leaf attacks per minute divided by the pooled
number of searches (i.e., all search maneuvers) per minute, of all
focal bird species per tree species. If an individual bird used multi-
ple trees during a foraging observation session, we used data from
each tree species to calculate the tree-species specific leaf attack
index. A unique leaf attack index was computed for each tree
and a higher leaf attack index indicated greater foraging success
per search effort on that tree species than on a tree species with
a lower leaf attack index.

To investigate the strength of the relationship between foraging
success and leaf petiole length, we calculated Spearman's rho for
the leaf attack index and average leaf petiole length, for each of ele-
ven tree species. Leaf attack indices and leaf petiole length from
trees that were morphologically similar, such as American and
slippery elm, and red and sugar maple, were combined for this
analysis in an effort to minimize autocorrelation (i.e., inflated de-
grees of freedom). Leaf attack indices and leaf petiole length from
trees that were similar taxonomically yet morphologically unique,
such as northern red and white oak were considered independent.
All statistical analysis was completed using the R statistical soft-
ware package (R Development Core Team, 2005).

3. Results

3.1. Tree preferences and foraging substrates used by migratory songbirds

We recorded 176 focal species foraging observations over the
duration of 363 min in 2009 and 127 observations over the dura-
tion of 178 min in 2010. We found the focal species to be highly
selective in their tree use ($\chi^2 = 160.03$, df_{10} , p -value = <0.001,
Fig. 2). Trees which were used in greater proportion than their
availability during both 2009 and 2010 included slippery elm
(63% more than if it were used in proportion to its availability), pa-
per birch (57% more), northern red oak (52% more), white oak (47%
more), American elm (41% more), and big-tooth aspen (30% more,
Fig. 2). Trees which were used in lower proportion than their avail-
ability in both years included basswood (96% less than if it were
used in proportion to its availability), black cherry (*Prunus serotina*,
86% less), red maple (81% less), bur oak (*Quercus macrocarpa*, 73%

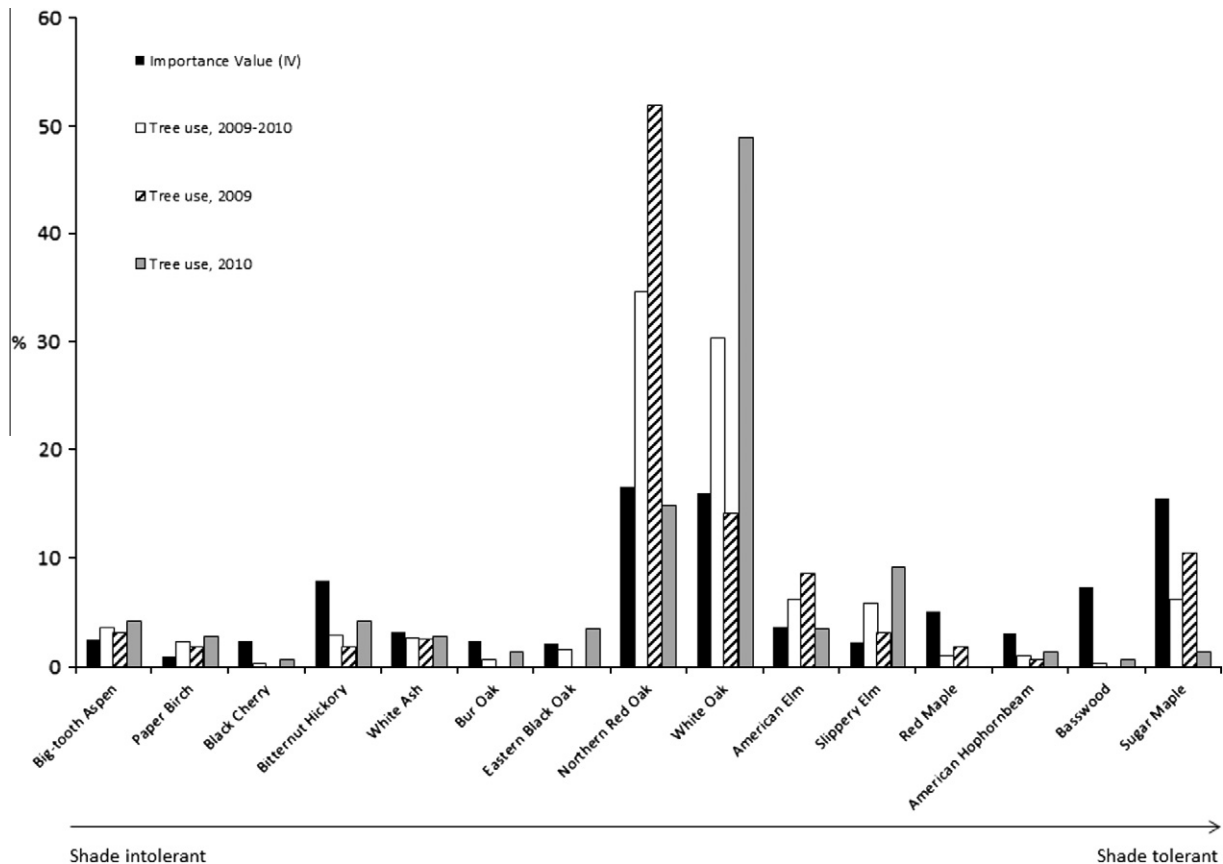


Fig. 2. Current period importance value of tree species juxtaposed with proportional use of each tree species by all foraging migratory songbirds in 2009 and 2010. Fifteen tree species were included to show foraging preferences of bird species on trees that were either common in 2010 or in the 1840s.

less), American hophornbeam (*Ostrya virginiana*, 69% less), bitternut hickory (63% less), and sugar maple (60% less, Fig. 2). There was variation in use of some trees species by focal birds between 2009 and 2010 (Fig. 2). There was a reduction of use of sugar maple (86%), northern red oak (71%), and American elm (59%), and an increase in use for white oak (71%), slippery elm (67%), American hophornbeam (56%), and bitternut hickory (56%) from 2009 to 2010 (Fig. 2). Eastern black oak (*Quercus velutina*), basswood, and black cherry were not used in 2009 but were used in 2010, with eastern black oak being used in higher proportion than it was available. Red maple was used in 2009 but not 2010.

Three patterns of tree-species preferences emerged. Focal species consistently avoided sugar maple, red maple, basswood, and bitternut hickory (Table 3). Second, northern red oak, white oak, slippery elm, and to a lesser extent, American elm, paper birch, and big-tooth aspen were consistently preferred (Table 3). Third, the foraging attacks of focal species were directed at specific ephemeral tree phenophases (e.g., budburst or flowering, Table 4). For example, although focal species largely avoid sugar maple, they do direct attacks at the buds of this tree species early in the spring before the leaves are fully flushed (EMW personal observation, Table 4). The male flowers (i.e., catkins) of northern red and white oak were highly important foraging substrates for focal species (Table 4). However the majority of attacks on most tree species were directed at the leaf surface (Table 4).

3.2. Factors affecting foraging success by migratory songbirds

We found strong support for the hypothesis that the differential accessibility of invertebrate prey among tree species influences foraging success by focal species ($\rho = -0.96$, p -value < 0.001,

Fig. 3). The leaf attack index was higher on trees with smaller leaf-petiole lengths such as white ash, American and slippery elm, paper birch, and white and northern red oak than on trees with larger leaf-petiole lengths such as basswood and maples (Table 4, Fig. 3).

3.3. Historic changes in availability of tree foraging substrates for migratory songbirds

In PLSS 1840s data, 21 tree species were recorded in the Kickapoo Valley Region, while during 2010 surveys 32 tree species, and 22 sapling species were recorded in the Kickapoo Valley Reserve. The most important tree species in the Kickapoo Valley Region in the 1840s were sugar maple (30%), white oak (24%) and basswood (13%, Fig. 4). The most important tree species in 2010 were northern red oak (17%), white oak (16%), and sugar maple (16%, Fig. 4).

Although never common, red pine (*Pinus resinosa*, 100% reduction) and butternut (*Juglans cinerea*, 86% reduction) suffered the greatest magnitude of reduction from the 1840s to 2010. Other species that were at least a third less important from the 1840s to 2010 were eastern black oak (49% reduction), sugar maple (49% reduction), basswood (44% reduction), white oak (34% reduction), bur oak (31% reduction), and elm species (30% reduction, Fig. 4). Trees species that were at least two-thirds more important in 2010 than in the 1840s included hickory species (mainly bitternut hickory, 91% increase), northern red oak (86% increase), eastern white pine (*Pinus strobus*, 72% increase) and white ash (66% increase, Fig. 4). Sapling composition, an indicator of the future tree-species composition in the region, was dominated by sugar maple, which made up 69% of all saplings recorded (Fig. 4). Most other tree saplings were encountered in low densities (<5%).

Table 3
Tree-species preference (positive) and aversion (negative) by eight migratory songbird species during spring migration. Trees ordered by shade tolerance with shade-intolerant trees listed first.

| Tree species | Migratory songbirds | | | | | | | | Total |
|-------------------|---------------------|--------|--------|-------|-------|-------|-------|--------|--------|
| | BGGN | BLBW | BTNW | BWWA | CSWA | MYWA | NAWA | TEWA | |
| Big-tooth aspen | 6.74 | -2.79 | -2.79 | -2.79 | -2.79 | 1.06 | 0.66 | 1.61 | 0.53 |
| Paper birch | 3.67 | -1.09 | 10.02 | -1.09 | -1.09 | -1.09 | 2.36 | -1.09 | 0.99 |
| Bitternut hickory | -3.92 | -3.68 | -8.68 | -8.68 | 1.32 | -4.83 | -1.78 | -7.58 | -5.77 |
| White ash | 1.22 | -3.55 | 0.16 | 2.34 | -3.55 | -3.55 | -0.10 | 0.85 | -0.23 |
| Northern red oak | 5.59 | 61.78 | -3.40 | 5.31 | 21.78 | 4.86 | 5.92 | 26.84 | 17.88 |
| White oak | 6.24 | -2.57 | 26.87 | -5.81 | 2.43 | 28.58 | 13.46 | 8.80 | 11.06 |
| American elm | 0.73 | -4.03 | 7.08 | 1.85 | 5.97 | -4.03 | -4.03 | 4.76 | 1.78 |
| Slippery elm | -2.41 | -2.41 | 1.29 | 21.12 | -2.41 | -2.41 | 11.38 | 4.18 | 3.81 |
| Red maple | -5.62 | -5.62 | -1.92 | 0.26 | -5.62 | -5.62 | -5.62 | -5.62 | -4.79 |
| Basswood | -8.08 | -8.08 | -8.08 | -8.08 | -8.08 | -4.24 | -8.08 | -8.08 | -7.67 |
| Sugar maple | -12.21 | -16.97 | -16.97 | 0.68 | -6.97 | 2.26 | -3.18 | -15.87 | -10.75 |

Table 4
Mean (\pm standard error) summary of migratory songbird search effort and foraging attacks per minute for eleven tree species. We included only the most common search maneuvers and tree characteristics on which attacks were centered. Bud, flower, or leaf refers to an attack (e.g., lunge glean) on the corresponding tree characteristic. Total search and attack are a composite of all search maneuvers (e.g., shuffle) and attacks (e.g., bark glean). Leaf attack index is a measure of food accessibility and refers to observed number of leaf attacks divided by total search maneuvers, per minute. Higher leaf attack index values indicate greater success (prey items ingested) per search effort. Trees ordered by shade tolerance with shade-intolerant trees listed first.

| Tree species | Migratory songbird search effort | | | | Migratory songbird foraging attacks | | | | Leaf attack index |
|-------------------|----------------------------------|--------------|-------------|--------------|-------------------------------------|-------------|-------------|---------------|-------------------|
| | n^{seconds} | Hops | Flights | Total search | Bud | Flower | Leaf | Total attacks | |
| Big-tooth aspen | 23 ¹⁶⁸⁷ | 9.84 (1.45) | 4.80 (0.65) | 14.64 (1.76) | 0.67 (0.52) | 0.41 (0.18) | 0.52 (0.30) | 1.60 (0.63) | 0.04 |
| Paper birch | 7 ⁸⁴⁶ | 10.92 (0.99) | 3.04 (0.60) | 13.96 (0.94) | 0.26 (0.26) | 0 | 1.95 (0.47) | 3.41 (0.41) | 0.14 |
| Bitternut hickory | 11 ⁹⁹⁰ | 14.92 (3.63) | 5.17 (1.42) | 20.09 (4.55) | 0.30 (0.30) | 0 | 0.89 (0.39) | 3.18 (0.50) | 0.04 |
| White ash | 13 ¹¹¹² | 7.90 (1.38) | 3.45 (0.97) | 11.34 (1.81) | 0 | 0 | 2.91 (0.81) | 3.05 (0.84) | 0.26 |
| Northern red oak | 140 ¹²¹⁶⁹ | 10.63 (0.51) | 3.38 (0.30) | 14.02 (0.60) | 0.14 (0.06) | 1.36 (0.19) | 1.76 (0.24) | 3.56 (0.28) | 0.13 |
| White oak | 98 ⁷⁰⁸⁰ | 9.74 (0.84) | 3.39 (0.41) | 13.13 (1.07) | 0 | 1.35 (0.23) | 2.10 (0.33) | 3.69 (0.39) | 0.16 |
| American elm | 21 ²⁴¹³ | 11.84 (1.37) | 2.22 (0.35) | 14.06 (1.47) | 0 | 0 | 2.09 (0.45) | 2.62 (0.51) | 0.15 |
| Slippery elm | 18 ¹³¹⁹ | 9.73 (2.41) | 4.40 (0.81) | 14.13 (2.50) | 0 | 0 | 4.15 (0.92) | 4.36 (0.92) | 0.29 |
| Red maple | 10 ⁶⁶⁹ | 9.39 (1.75) | 4.15 (1.09) | 13.54 (2.01) | 0.10 (0.10) | 0 | 0.45 (0.35) | 0.69 (0.38) | 0.03 |
| Basswood | 7 ⁴²⁴ | 11.84 (3.13) | 3.50 (1.05) | 15.34 (3.84) | 0 | 0 | 0.38 (0.31) | 0.92 (0.42) | 0.02 |
| Sugar maple | 35 ²²⁸¹ | 8.23 (1.20) | 6.01 (1.36) | 14.25 (1.52) | 0.59 (0.33) | 0 | 0.31 (0.12) | 1.74 (0.41) | 0.02 |

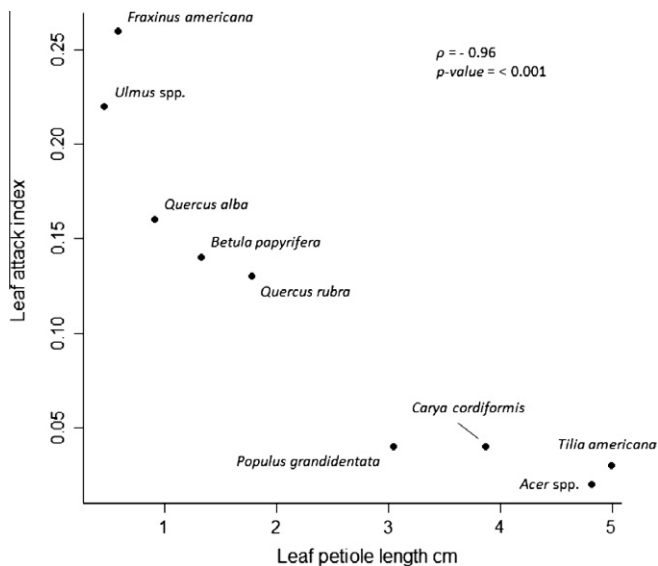


Fig. 3. Scatter plot and Spearman's rho correlation (ρ) of leaf petiole length (cm), an indicator of food accessibility, of nine tree species or groupings of trees (e.g., *Acer* spp.) versus migratory songbird leaf attack index. Tree species were selected for this analysis because they were either frequently used as foraging substrates by migratory songbirds or were commonly encountered in our study.

4. Discussion

Our results suggest the future dominance of forest composition by shade-tolerant tree species will likely negatively impact stop-

over habitat quality for migratory songbirds. We found eight migratory songbirds used moderately shade tolerant tree species, such as northern red and white oak, and slippery and American elm, as well as shade-intolerant tree species such as big-tooth aspen, and paper birch as foraging substrates during spring migration in greater proportion than their availability. These same bird species strongly avoided shade-tolerant tree species, such as red and sugar maple, and basswood. These findings are consistent with tree preferences of migratory songbirds during the breeding season in New Hampshire forests, where Holmes and Robinson (1981) discovered eight of ten bird species avoided sugar maple and preferred an intermediate shade tolerant tree, yellow birch (*Betula alleghaniensis*). Similarly, our findings support results from spring migration in Illinois woodlots and forest, where Graber and Graber (1983) and Strode (2004) documented the high use of oak and elm species and the low use of sugar maple and basswood by migratory songbirds.

In general, forest composition in our study region remains dominated by sugar maple and oaks. However, the importance of oaks has shifted. While white oak is still an important tree of Driftless Area forests, it has decreased, which is a pattern common throughout eastern deciduous forests (Abrams, 2003). Bur and eastern black oak are also losing importance in the region, which is indicative of loss of the forest openings and savanna habitats in which these species are found (Curtis, 1959; Nuzzo, 1986). Therefore, if there is an increase in shade-tolerant species, eastern black and bur oak will most likely be extirpated from the Driftless Area except for in managed areas, or locations where shade-tolerant trees grow poorly (e.g., sandy soils, Curtis, 1959). Our evidence that white oak, and to a lesser extent eastern black oak are important

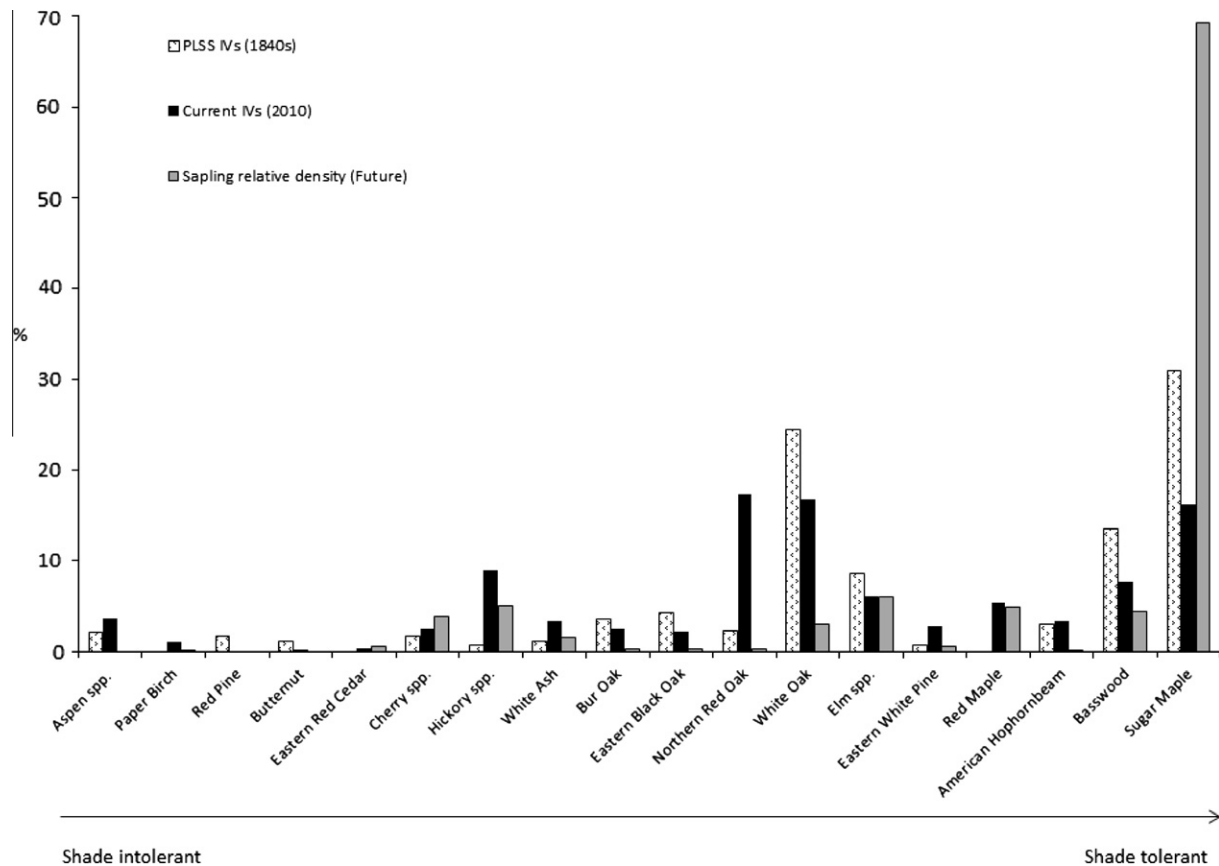


Fig. 4. Public Land Survey System 1840s witness tree importance values (PLSS IVs), current tree IVs (2010), and sapling relative density (an indicator of future importance) within the Kickapoo Valley Region.

foraging resources suggests that these tree species, which were once more common in the region, were potentially historically important foraging resources for migratory songbirds during spring migration at stopover locations.

Northern red oak was far more common in 2010 than in the 1840s, because it became established in forested stands after intense logging operations during the late 1800s and early 1900s (Nowacki et al., 1990). Northern red oak is a relatively fast growing tree (Lorimer, 1983) and many of the specimens in our study region were super-canopy trees, (i.e. crowns extend above the surrounding canopy; EMW personal observation). This may have contributed to the high-quality of northern red oak as foraging substrate because the canopy is exposed to more sunlight and wind (Terborgh, 1985). These conditions are associated with catkins (Keator, 1998), which were heavily preferred by migratory songbirds. However, we found only one northern red oak sapling highlighting that this species is likely a dominant tree for only a single generation (Nowacki et al., 1990). Thus as the current mature trees senesce, a critical foraging resource for migratory songbirds is dropping out of Driftless Area forests.

Slippery and American elm, which were both important resources for foraging migratory songbirds, appear to be regenerating well. Although American elm will never again be a dominant canopy tree due to Dutch elm disease (Schlarbaum et al., 1997), both elm species will most likely remain at a low but constant level of importance as part of the canopy (slippery elm) and sub-canopy (both American and slippery elm) in the Driftless Area forests. Two other species that were important foraging substrates, big-tooth aspen and paper birch, are early successional trees (Curtis, 1959) and are regenerating poorly. Without disturbance (e.g., fire) or management, these species will likely disappear from the region

further reducing the availability of desirable foraging substrates for migratory songbirds during spring migration.

Shade-tolerant tree species, which were avoided by foraging migratory songbirds, have also shifted in importance from the 1840s to 2010. Sugar maple and basswood declined, and red maple increased in importance. Basswood and sugar maple typically grow in mesic conditions (e.g., north facing slopes) and can grow to large sizes in the Driftless Area (Curtis, 1959). Sugar maple is a valuable timber product (Allen et al., 1999) and it is likely this species was also harvested in the Driftless Area forests following Euro-American settlement. Our finding that red maple has dramatically increased in importance throughout our study region echoes similar trends for this species throughout eastern North American forests (Lorimer, 1984; Abrams, 1998), and is of concern because red maple was avoided by foraging migratory songbirds in this study.

We found a large increase in bitternut hickory importance from the 1840s to 2010. Bitternut hickory is moderately tolerant of shade and is able to grow on poor sites (e.g., steep, well drained soils, Curtis, 1959). We speculate that bitternut hickory is able to become established on poor sites where shade-tolerant trees do not grow well and because it is a fast growing tree (Hix and Lorimer, 1990). Once established, it may outcompete saplings that need ample light for growth. We did not find evidence that focal species preferred bitternut hickory as a foraging substrate as was found in Illinois woodlots during spring stopover (Strode, 2004) and floodplain forest during the breeding season (Gabbe et al., 2002).

Sugar maple, red maple, basswood, and bitternut hickory were used less than expected given their availability in the region by migratory songbirds, but these species are regenerating well in

our study region, and therefore will likely dominate the future forest of the Driftless Area. These results are consistent with findings from other work in the region (Hix and Lorimer, 1991; Rogers et al., 2008). Furthermore, these trends in regeneration follow a common pattern of forest succession in eastern mixed-hardwood forests since Euro-American settlement from white oak, to northern red oak, to dominance by mesophytic tree species (Abrams and Copenheaver, 1999). Although sapling regeneration was the best index of future forest available for this study, we realize that many potential factors may conspire to cause mortality of these saplings (e.g., deer and rabbit browsing, climate change, and introduced species). Therefore the future forest composition may not be reflected by this current sapling composition. Nevertheless, whether migratory songbirds can adapt their foraging patterns to the changing forest composition of the Upper American Midwest is not clear.

We expected migratory songbirds to use trees as foraging substrates in varying proportions than they were available. However, we were surprised to find dramatic differences in migratory songbird foraging behavior for individual tree species between the two study seasons. A plausible explanation for this was due to large differences in tree phenology between years. Tree species began flowering and growing leaves upwards of three weeks earlier in 2010 than 2009 due to mild winter and early spring conditions. This may have influenced food availability (Graber and Graber, 1983) and accessibility (Whelan, 2001) and in turn presented obstacles (e.g., longer petioles requiring energy intensive search efforts) that altered foraging behavior. Similar to the effect of flowering honey mesquite (*Prosopis glandulosa*) on migrating wood-warblers in an Arizona wash (McGrath et al., 2008), variation of spring tree phenophases in Driftless Area forests possibly influences food accessibility and proximate cues that foraging migratory songbirds use to the presence of prey items. For example, northern red oak trees generally flower two to three weeks earlier than white oak trees in our study system (EMW personal observation). Peak abundance of migratory songbirds occurs during the early and middle parts of May throughout southern Wisconsin (Temple et al., 1997). In 2009, northern red oak trees flowered at this time and were heavily used by migratory songbirds, whereas white oak trees did not flower until the middle and end of May and were not heavily used. In 2010, northern red oak reached summer condition (e.g., withered catkins and large mature leaf surfaces) by early May whereas white oak trees were flowering at this time. It is possible that migratory songbirds used white oak in much higher frequencies in 2010 rather than northern red oak because the oak catkins were a proximate cue to the availability of prey items. These findings offer clues regarding how variations in spring tree phenology possibly affect tree preferences by migratory songbirds.

We found strong support for the hypothesis that food accessibility (average leaf-petiole length) was influential in determining foraging success of migratory songbirds during spring migration. The majority of focal species foraging for prey-items were observed hopping toward the end of a branch, then lunge glean prey from a bud, leaf, or flower surface. This is in contrast to some breeding birds that display more plasticity in their foraging maneuvers and behaviors. For example, Robinson and Holmes (1984) found Red-eyed Vireo (*Vireo olivaceus*) and American Redstart (*Setophaga ruticilla*) in New England deciduous forests deploy various hovers, gleans, and flight pursuits depending on tree foliage structure and prey type. On the other hand, in the same study, Black-throated Blue Warbler (*Setophaga caerulescens*) was less variable in their search tactics among tree species with different foliage structure. Although these breeding migratory songbirds display plasticity in their foraging behavior (Robinson and Holmes, 1984), it is unclear if *en route* migratory songbirds are able to exploit resources

in an efficient manner among tree species that are structurally disparate.

Our finding that migratory songbirds have higher foraging success on trees with shorter leaf petioles follows predictions of optimal foraging theory, in which birds would be expected to forage in a way that maximizes their caloric intake while minimizing competing risks (Pyke, 1984). These results were similar to those found for breeding migratory songbirds foraging in a New England forest where yellow birch (*Betula alleghaniensis*) and American beech (*Fagus grandifolia*) were used more than expected given their importance in the landscape (Holmes and Robinson, 1981) and in an Illinois floodplain forest where bitternut and kingnut hickory (*Carya laciniata*) were also used more than expected given their importance in the landscape (Gabbe et al., 2002). These tree species all have relatively short petioles (Sibley, 2009). However sycamore (*Platanus occidentalis*) was also used more than expected given its importance in the landscape (Gabbe et al., 2002), making an apparent exception to the observation that short petioles are associated with greater foraging success. Additional factors such as prey abundance or prey size likely also contribute to tree species foraging preferences (Robinson and Holmes, 1982).

Whelan (2001) experimentally tested different foraging strategies in relation to foliage structure for breeding American Redstart, Black-throated Green Warbler, and Black-throated Blue Warbler captured in New England forests. He found distance to prey (e.g., arrangement of prey item with respect to petiole length and leaf placement) determined prey capture maneuverers (i.e., aerial vs. non-aerial). The three species used non-aerial attacks for closer prey items and aerial attacks for prey items that were further away. Thus, in the case of trees with long leaf-petioles, like maples and basswood, it may either not pay off energetically for birds to perform aerial maneuvers to reach prey, or it may be physically difficult for some species to perform some aerial search maneuvers (e.g., hover glean). Therefore, we suggest spring migratory songbirds are likely selecting tree species as foraging substrates that are amicable for effective foraging. This, in turn, influences efficient migration body condition (Moore and Kerlinger, 1987) and ultimately governs optimal arrival times at the breeding grounds (Moore et al., 2005).

Our findings offer important clues why increases in shade-tolerant tree species may result in decreased stopover habitat quality for spring migratory songbirds. For example, sugar maple has long, rigid petioles (Robinson and Holmes, 1984; Beaudet and Messier, 1998), which is an adaptation of some shade-tolerant species to support large leaves to maximize their ability to capture sunlight in dark conditions (Takenaka et al., 2001). Thus, as forest succession moves towards dominance by shade-tolerant species, there will likely be a decrease in stopover habitat quality for migratory songbirds due to non-optimal foraging conditions (i.e., difficult to access prey items). This is of particular concern because, in addition to decreased foraging success, bird species will likely also contend with less optimal foraging substrates. Oaks are regenerating poorly, elm species are decreasing as a canopy dominate, and ash species are in danger due to emerald ash borer beetle (*Agrilus planipennis*). In contrast, shade-tolerant species are regenerating well. Furthermore, Wisconsin forests are approximately the 'last stop' for many migratory songbird species before reaching the breeding grounds. It has been suggested that at this stage in spring migration, birds increase their fat reserves, compromising their flight efficiency, in order to boost energy reserves needed for breeding period demands (e.g., mate selection, Sandberg, 1996; Sandberg and Moore, 1996; Fransson and Jakobsson, 1998; Moore et al., 2005; Smith and Moore, 2005). Thus, our work also offers additional clues to problems affecting migratory songbirds on the breeding grounds.

5. Conclusions

Although we expected to see larger differences in tree species composition between the 1840s to the current time, our results suggest a future shift in tree-species composition of Upper American Midwest forests toward dominance by shade-tolerant species. This coupled with our findings of tree preference and aversion by migratory songbirds suggests the future forest will have lower quality foraging resources for these birds. We found that oak and elm, and to a lesser extent, big-tooth aspen, paper birch, and white ash are valuable foraging substrates for migratory songbirds and these trees are being lost from the Upper American Midwest landscape. Furthermore, we found migratory songbirds have higher foraging success on tree species with shorter leaf petioles, suggesting food accessibility is a factor limiting migratory songbird foraging success during spring migration. It is not clear how successful migratory songbirds can be in finding high quality foraging substrates as forest composition continues to change toward dominance by shade-tolerant species. For effective conservation of migratory songbird stopover habitat in Upper American Midwest hardwood dominated forests, efforts should be made to maintain oak, elm, and other early successional tree species (e.g., big-tooth aspen) on the landscape.

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