TREE REGENERATION IN A SOUTHWESTERN INDIANA FOREST: IMPLICATIONS OF LONG-TERM BROWSING BY DEER

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ABSTRACT.   Wesselman Woods Nature Preserve (WWNP) has never been subjected to timber harvest. However, deer can completely penetrate WWNP and browse tree seedlings and saplings throughout the forest. In this study, 30 plots (20 × 30 m) were surveyed (1.8 ha total). All trees of every size were identified and categorized into one of four strata based on height—herb layer, shrub layer, midstory, and overstory. Using the Shannon-Weiner Diversity Index, diversity was compared across strata. In the midstory 95% of stems over 150 cm in height and with a dbh < 5 cm) were pawpaws (3841 of 4038 stems). Sugar maples comprised 101 of the remaining midstory trees, and only three other species had more than 10 trees in this stratum. Oak trees had been almost completely lost from the midstory. Given its poor representation of canopy species, the midstory layer had significantly lower diversity compared to other strata. Many tree species (including sweetgum, tulip poplar, blackgum, hackberry, and 12 species of oak) have not transitioned into the midstory stratum, suggesting that regeneration of these species into the overstory is limited. In addition, pawpaw appears to have formed a recalcitrant layer and is anticipated to limit forest regeneration even more. While the patterns observed in this survey suggest that forest regeneration may be constrained by deer browsing at WWNP, an experimental study would be needed to confirm that deer (versus other factors, such as fire suppression or shading conditions of the forest) are responsible for limited regeneration. Placed within a forest management perspective, we discuss one possible experiment to examine concerns related to deer browsing and overabundance of pawpaw trees.

Keywords: *Acer*, *Asimina triloba*, pawpaw, *Odocoileus virginianus*, *Quercus*, deer browsing, Wesselman Woods Nature Preserve

INTRODUCTION

Herbivores alter the composition of plant communities (Augustine & McNaughton 1998; Olff & Ritchie 1998), and mammalian herbivores can have profound effects on their habitats (Augustine & McNaughton 1998; Knapp et al. 1999; Fortin et al. 2005; Pringle 2008; Martin et al. 2010, 2011). White-tailed deer (*Odocoileus virginianus* Zimmerman) populations in the eastern United States have been large enough that browsing by white-tailed deer (hereafter referred to as deer) has degraded the quality of many forest communities (reviewed by McShea et al. 1997). In particular, high deer density threatens tree regeneration (reviewed by Russell et al. 2001; Horsley et al. 2003; Rooney et al. 2004; Comisky et al. 2005; Rossell et al. 2005; Griggs et al. 2006; Long et al. 2007; Goetsch et al. 2011; Kain et al. 2011; Abrams & Johnson 2012; Chollet et al. 2013; Shelton et al. 2014). Browsing alters the physical structure of forests, causing reductions in

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stem/foliar density, as well as limiting sapling height. While deer browsing suppresses seedling/sapling establishment, preferential browsing also commonly occurs among woody species. By governing changes in woody species diversity in the forest understory, browsing by deer can potentially shift the future canopy forest community.

Deer browse on a wide range of tree species, including both evergreen and deciduous species. Still, oak species, which are commonly dominant/co-dominant canopy species in Midwestern forests (Dyer 2006), are especially at risk because deer greatly prefer to browse on oaks (Rooney & Waller 2003; Rossell et al. 2005; Long et al. 2007; Wakeland & Swihart 2009). While preferential browsing severely limits oak regeneration (Rooney & Waller 2003; Rossell et al. 2005; Belden & Pallardy 2009; Abrams & Johnson 2012), maples often experience browsing only when more preferred species are no longer available, leading to maples becoming more common in forests browsed by deer (Anderson & Katz 1993; Rooney & Waller 2003; Belden & Pallardy 2009).

While these problematic changes are a concern for all forests in the eastern United States, the negative impact of deer may be of particular concern to virgin forests (i.e., old growth forests that have no history of being logged). Virgin forests can harbor high biodiversity, but such forests are rare (Fischer et al. 2013). In the state of Indiana, the Division of Forests lists only 11 old growth forests (i.e., forests containing trees of 150 years or older) owned by government agencies (IDNR-F 2016), and the Division has designated only three virgin forests (i.e., forests the Division describes as neither touched by human activity nor disturbed by unnatural factors) within the state.

The largest of these virgin forests is Wesselman Woods Nature Preserve (WWNP), which harbors more than 40 woody species (Table 1). At just under 80 ha, WWNP is a small forest tract, even though it is more than twice as large as either of the other two Indiana virgin forests. Nonetheless, small forests, even the size of WWNP, have relatively greater forest edge (Bowen & Burgess 1981) than historic forests of Indiana. Thus, the impact of deer, which favor foraging along forest edges (Alverson et al. 1988; Waller & Alverson 1997; Côté et al. 2004), can be exacerbated in our few remaining virgin forests.

To document the damage associated with high deer populations, studies have utilized exclosures (Alverson et al. 1988; Anderson & Katz 1993; Rossell et al. 2005; Griggs et al. 2006; Long et al. 2007; Goetsch et al. 2011; Abrams & Johnson 2012; White 2012), refuge areas (Comisky et al. 2005; Chollet et al. 2013), and areas with contrasting low deer populations (Horsley et al. 2003; Webster et al. 2005; Tremblay et al. 2007); however, few recent studies have probed the differences among canopy strata that may be caused by deer activity (but see Long et al. 2007). In part, pattern-based surveys are of limited utility because they lack experimental rigor, and so they lack the ability to discriminate among alternative explanations (Swihart et al. 2002). Still, descriptive comparisons between lower woody strata and the overstory can suggest whether constraints on forest regeneration may be associated chronic exposure to intense browsing regimes.

Decades of intensive deer browsing could also lead to the formation of a recalcitrant layer (*sensu* Royo & Carson 2006). Recalcitrant understory layers have been shown to affect regeneration, and deer browsing can facilitate the establishment of a recalcitrant layer (Tighman 1989; Stromayer

& Warren 1997; Goetsch et al. 2011; Tanentzap et al. 2009; Kain et al. 2011; Johnson et al. 2015). In turn, forest successional trajectories may be altered, potentially causing a compositional change in the overstory.

Pawpaw (*Asimina triloba* L.) may act as a recalcitrant layer. Pawpaw utilizes annonaceous acetogenins as chemical defenses against herbivores (Ratnayake et al. 1992; Harborne 2001; Arnason & Bernards 2010). While deer will browse other, less-palatable woody vegetation when more-palatable stems are gone, deer avoid browsing pawpaw plants (Wakeland & Swihart 2009; Slater & Anderson 2014). Pawpaw's unpalatable quality, coupled with its shade tolerance (Battaglia & Sharitz 2006) and its vegetative reproduction strategy (Hosaka et al. 2016), may allow pawpaw to form a recalcitrant layer. Slater & Anderson (2014) found that deer browsing led to a dense pawpaw understory as a result of decades of intensive deer browsing. Other studies have suggested that pawpaw may limit canopy tree regeneration (Shotola et al. 1992; Shelton et al. 2014).

To evaluate the possible impact of browsing by deer on the forest composition of WWNP, the tree community among forest strata was compared. If deer browse has been chronic and extensive, tree diversity should be greatest in the overstory (because the canopy is the repository of tree diversity), as well as in the lowest stratum (because of seed production from canopy trees would generate seedling diversity), and diversity should be least in the intermediate strata because preferential browsing by deer would act as a filter, limiting which species could grow beyond sapling height. In addition, the pattern of oak and maple abundance was examined, as well as basal area, among strata to lend support to the argument of preferential browsing by deer. The relative importance of oak was predicted to be greater in the overstory and lowest stratum compared to the two intermediate strata. Finally, pawpaw abundance across strata was examined, comparing its abundance (and basal area) to other woody species. For pawpaw to act as a recalcitrant layer, higher relative abundance of pawpaw should occur in lower forest strata.

METHODS

Study site & species.—Wesselman Woods Nature Preserve (WWNP) is a virgin forest (IDNR-F 2016), having never been harvested for timber. WWNP is designated as a sweet-

Table 1.—Tree species occurring at six sites in Wesselman Woods Nature Preserve. The number of trees observed within each stratum across 30 plots (1.8 ha) is given for each species. * = species not native to Indiana.

Species name	Common name	Herb layer	Shrub layer	Mid-story	Over-story
Acer negundo	boxelder	141	69	4	5
Acer rubrum	red maple	124	0	2	59
Acer saccharum	sugar maple	2027	74	101	277
*Ailanthus altissima**	tree-of-heaven*	0	1	0	0
Asimina triloba	pawpaw	7472	8689	3841	145
Carpinus caroliniana	musclewood	111	9	6	53
Carya cordiformis	bitternut hickory	254	4	3	1
Carya glabra	pignut hickory	1	0	0	0
Carya ovalis	red hickory	1	0	0	0
Carya ovata	shagbark hickory	63	3	2	3
Carya tomentosa	mockernut hickory	2	1	1	1
Catalpa speciosa	northern catalpa	0	0	0	3
Celtis laevigata	southern hackberry	1199	118	4	52
Cercis canadensis	redbud	1	0	0	0
Cornus florida	flowering dogwood	3	1	0	2
Crataegus mollis	downy hawthorn	13	2	1	1
Fraxinus americana	white ash	229	58	6	6
Fraxinus pennsylvanica	green ash	1594	316	14	2
Fraxinus profunda	pumpkin ash	493	30	13	7
*Ilex aquifolium**	English holly*	4	1	0	0
Ilex decidua	possumhaw	3	0	2	0
Juglans nigra	black walnut	0	0	0	1
Liquidambar styraciflua	sweetgum	92	24	2	74
Liriodendron tulipifera	tulip poplar	74	0	1	31
Morus rubra	red mulberry	53	13	2	0
Nyssa sylvatica	blackgum	314	251	8	44
*Paulownia tomentosa**	empress tree*	0	1	0	0
Platanus occidentalis	sycamore	0	0	1	0
Populus deltoides	cottonwood	2	1	0	1
Prunus serotina	black cherry	635	132	1	0
Quercus alba	white oak	236	3	0	6
Quercus bicolor	swamp white oak	2	2	0	1
Quercus falcata	southern red oak	1	0	0	0
Quercus macrocarpa	bur oak	1	0	0	1
Quercus michauxii	swamp chestnut oak	2	0	0	3
Quercus muhlenbergii	chinkapin oak	3	0	0	0
Quercus pagoda	cherrybark oak	19	0	0	0
Quercus palustris	pin oak	3	0	0	1
Quercus prinus	rock chestnut oak	1	0	0	0
Quercus rubra	northern red oak	77	4	1	4
Quercus shumardii	Shumard oak	34	0	0	2
Quercus velutina	black oak	3	0	0	1
Sassafras albidum	sassafras	139	31	3	7
Ulmus americana	American elm	99	3	16	181
Ulmus rubra	slippery elm	147	2	1	13

gum-tulip tree wet mesic lowland forest (*sensu* Jackson 1980) because the forest is a wet, nearly flat lowland forest, with a canopy dominated by sweetgum (*Liquidambar styraciflua* L.) and tulip poplar (*Liriodendron tulipifera*d L.) (Lindsey et al. 1969). WWNP is unique in southwest Indiana because of its exceptional tree diversity and maturity; it is still "representative of Indiana's original ecological conditions prior to human settlement" (Lindsey et al. 1969). While WWNP has one of the highest basal areas of any known forest in the

state, the 80 ha preserve is completely surrounded by the city of Evansville, and includes a nature center, one small parcel maintained in lawn, and two small parcels of secondary forest, as well as a trail system (WNS-NRC 2010). Drainage changes have occurred historically, but standing water still occurs in a patchwork of the forest throughout the wetter portions of the year.

While human activities noted above may have altered WWNP, evidence suggests that white-tailed deer (*Odocoileus virginianus*) may have greatly influenced this forest. In the 1990s, censuses estimated the population to be between 30 to 55 deer/km^2 (B. Fichter unpublished data; C.M. Norrick unpublished data; G. Hesselink unpublished data; Ribbens unpublished data). Still, the lack of forest regeneration at WWNP may have been a concern for at least 45 years. The dominant canopy species were already poorly represented in the sapling layer in the 1960s (Lindsey et al. 1969), deer populations have been high in Indiana for decades (IDNR-FW 2015), and deer hunting did not begin in the preserve until 1999 (N. Bogan Pers. Comm.).

Experimental design.—In the summer of 2015, five plots (20×30 m) nested within each of six sites were surveyed (1.8 ha in total). For each of the 30 plots, all individual trees in every forest stratum were identified to species and counted. For stems over 150 cm in height, diameter at breast height (dbh measured at 1.3 m) was recorded. Trees were placed into one of four forest strata based on height. The strata included the herb layer (stems under 50 cm in height), the shrub layer (stems ranging between 50–150 cm in height), the midstory (trees over 150 cm in height and with a dbh < 5 cm), and the overstory (trees with a dbh $\geq$ 5 cm).

Analyses.—For each forest stratum within each plot, diversity was calculated using the Shannon-Weiner Diversity Index (H') (Brower et al. 1990). H' considers the proportion of the total that occurs for each species (evenness), as well as the number of species and total number of individuals (richness). To evaluate whether the four forest strata differed in diversity, a nested, random effects ANOVA was performed using plots as random samples nested within sites, which were treated as random blocks within the forest (JMP 2015). A Tukey post-hoc test was performed to determine differences in diversity among forest strata. Because high pawpaw abundance would create lower evenness (and thereby potentially generate lower H' values) solely due to its high relative abundance and not because of its effects on the other species, the same analysis was performed using a data set where all pawpaws were removed from the analysis. This second analysis evaluated whether diversity differed among strata, ignoring the contribution of pawpaws to richness and evenness.

The primary concern with this approach of evaluating H' is the assumption that H' should be constant across the forest layers in the absence of deer browsing. While other factors can influence tree species diversity, our assumption is conservative; more tree species can colonize as seedlings than can establish in the shrub layer, grow into the midstory stratum, and establish in the canopy. Using this perspective, H' should shift from the largest value to smaller and smaller values as one moves from the lowest strata to the highest one. In contrast, if deer have preferentially browsed certain tree species, H' will be lower in the strata affected by deer and higher in the canopy layer (where the community was established prior to the increase in deer abundance).

For each genus of tree, number of individuals was tallied across all plots (1.8 ha in total), and relative density was calculated for each stratum (Brower et al. 1990). In addition, dbhs were used to calculate basal area (m^2/ha) and relative basal area for the midstory stratum and the overstory. The relative importance of oak and maple abundance and basal area among strata was quantified by dividing the number (or basal area) of oaks by the total number (or basal area) of oaks and maples.

Finally, relative pawpaw abundance was compared across strata. For these comparisons, the shrub layer would be expected to include stems that have escaped browsing by deer just recently (a few years), while stems in the midstory would have grown taller than deer could browse many years ago, and trees in the overstory would have escaped the risk of browsing by deer at a much earlier time.

RESULTS

More than 40 native tree species were identified across the four strata (Table 1). Forty-one species were found in the herb layer, with an average of 13.7 species per plot. In the shrub layer, 27 species were found, with an average of only 5.3 species per plot. The midstory had a very low average of 3.5 species per plot, and only 24 species were

identified. Finally, 31 species occurred in the overstory, with an average of 7.2 species per plot.

With pawpaws included in the analysis, the Shannon-Wiener Diversity Index (H') was 1.53 ± 0.07 ($\bar{X} \pm$ SE) in the herb layer, 0.49 ± 0.08 in the shrub layer, 0.26 ± 0.04 in the midstory, and 1.43 ± 0.07 in the overstory. The statistical model was significant ($F_{32,87} = 9.2$; $P < 0.0001$), and significant differences were detected among the four forest strata ($F_{3,87} = 88.3$; $P < 0.0001$). While the overstory was not significantly different from the herb layer, both were significantly higher in diversity than either the shrub layer or the midstory layer (Fig. 1A).

With pawpaws excluded from the analysis, H' was 1.73 ± 0.06 in the herb layer and 1.15 ± 0.10 in the shrub layer. H' was 0.76 ± 0.10 in the midstory stratum and 1.37 ± 0.08 in the overstory. This statistical model was significant ($F_{32,87} = 3.8$; $P < 0.0001$), and significant differences were detected among the four forest strata ($F_{3,87} = 25.3$; $P < 0.0001$). The herb layer had significantly higher diversity than overstory and shrub layers, while both were significantly higher in diversity than the midstory layer (Fig. 1B). Thus, the midstory layer had significantly lower diversity compared to all other strata.

In the herb layer, 380 oaks (including individuals from 13 species) were found across the six areas sampled. Nineteen oak trees (of eight species) were found in the overstory. Still, just nine individual oak trees were observed in the shrub layer, and only a single oak tree was found in the midstory stratum (Table 2). This limited number of oak trees in the shrub layer and midstory stratum prevented statistical comparisons regarding the relative importance of oaks and maples. However, the pattern of their relative abundance is strongly suggestive. When considering the relative number of trees that were oaks (with only oaks and maples included in the calculations), 5% of trees in the overstory were oaks, 6% of trees in the shrub layer were oaks, and 14% of trees in the herb layer were oaks; however, only 1% of trees in the midstory was oaks, while 99% were maples. The comparison between oaks and maples is similarly striking when considering basal area. Oaks constituted only 1% of the basal area in the midstory, whereas maples comprised the other 99%. However, oaks made up 45% of basal area in the overstory, compared to maple, which comprised 55%.

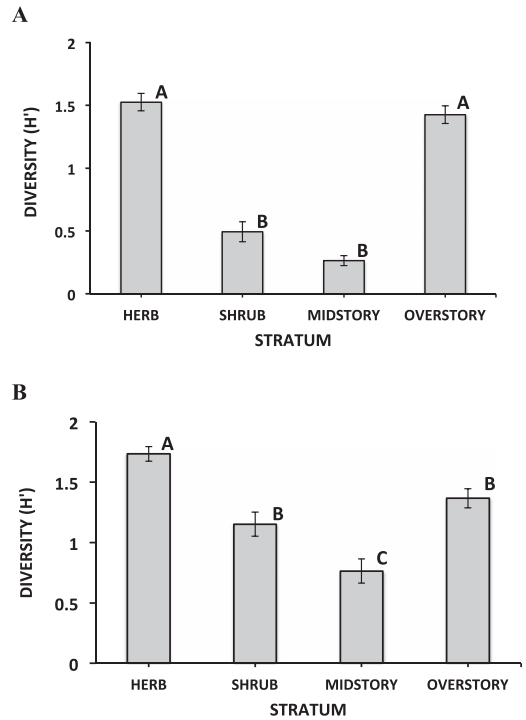Nearly two-thirds (20,150 of 30,548) of all stems surveyed were pawpaws (Table 2). Paw-

Figure 1.—Bar graph representing mean diversity ($\pm$ SE) for four forest strata using the Shannon-Weiner Diversity Index (H'). A. When pawpaw was included in the estimate of diversity, and B. When pawpaw was excluded. Strata were designated as herb layer (trees of under 50 cm in height), the shrub layer (trees ranging between 50–150 cm in height), the midstory (trees over 150 cm in height and with a dbh < 5 cm), and the overstory (trees with a dbh ≥ 5 cm). Different letters designate significant differences among strata.

paws were the most abundant species in every stratum except the overstory. In contrast, two other traditional sub-canopy specialists (flowering dogwood and redbud) had fewer than five individuals across all plots in all strata combined. Musclewood (*Carpinus caroliniana* Walter), another subcanopy specialist, was reasonably abundant, with 179 individuals across the four strata. Even musclewood, though, had more than 90% of its stems occur in the overstory or herb layer, not in the shrub and midstory strata.

Two genera beside pawpaw were well represented: maple and ash (Table 2). Maple (sugar maple, red maple, and boxelder) was the second most abundant genus, with 2,875 individuals. Sugar maples comprised 2,485 of those stems (Table 1). Ash (green, pumpkin, and white ash)

Table 2.—Summary information for genera that contributed to each forest stratum. Number represents the number of individuals within the sampled area of 1.8 ha (30 plots). Relative density was calculated for each species as a percentage of the total number of individuals of all species. Basal area was determined for each species as the cumulative area of all trees of a given species at breast height. Basal area was scaled to m^2/ha. Relative basal area was calculated for each species as a percentage of the total basal area of all species within a given stratum.

Genus	Number				Rel. density				Basal area		Rel. basal area	
	Herb layer	Shrub layer	Mid-story	Over-story	Herb layer	Shrub layer	Mid-story	Over-story	Mid-story	Over-story	Mid-story	Over-story
Asimina	7472	8689	3841	145	47.7%	88.3%	95.1%	14.7%	0.599	0.30	87.1%	0.8%
Acer	2292	143	107	341	14.6%	1.5%	2.6%	34.5%	0.057	6.06	8.2%	15.2%
Quercus	380	9	1	18	2.4%	0.1%	0.0%	1.8%	0.000	4.96	0.0%	12.4%
Liquidambar	92	24	2	74	0.6%	0.2%	0.0%	7.5%	0.001	14.59	0.1%	36.5%
Liriodendron	74	0	1	31	0.5%	0.0%	0.0%	3.1%	0.000	5.20	0.0%	13.0%
Nyssa	314	251	8	44	2.0%	2.6%	0.2%	4.5%	0.003	3.74	0.4%	9.3%
Ulmus	246	5	17	194	1.6%	0.1%	0.4%	19.7%	0.011	1.74	1.6%	4.4%
Fraxinus	2316	404	33	15	14.8%	4.1%	0.8%	1.5%	0.006	1.12	0.9%	2.8%
Celtis	1199	118	4	52	7.7%	1.2%	0.1%	5.3%	0.002	0.90	0.3%	2.3%
Carpinus	111	9	6	53	0.7%	0.1%	0.1%	5.4%	0.004	0.29	0.6%	0.7%
Carya	321	8	6	5	2.0%	0.1%	0.1%	0.5%	0.003	0.16	0.4%	0.4%
Sassafras	139	31	3	7	0.9%	0.3%	0.1%	0.7%	0.000	0.41	0.0%	1.0%
Prunus	635	132	1	0	4.1%	1.3%	0%	0%	0.000	0	0%	0%
Other	79	20	8	8	0.5%	0.2%	0.5%	0.8%	0.002	0.48	0.3%	1.2%

was the third most abundant genus, with 2,768 individuals. Green ash comprised 1,926 of those individuals. These three genera (pawpaw, maple, and ash) encompassed 84.5% of all recorded stems. Still the importance of species varied with forest strata. In the midstory stratum, pawpaws were nearly mono-dominant, with a striking 95% of stems being pawpaws (Table 2). Pawpaws were also extremely important in the shrub layer, at 88%. Pawpaws were less important in the herb layer, with fewer than 50% of stems being pawpaws. Only in the overstory were pawpaws, at 15%, not the most abundant tree.

Pawpaws comprised 87% of the basal area in the midstory (Table 2). In contrast, pawpaw contributed only 0.8% of the basal area to the overstory, even though it was third highest for abundance in the overstory. Only maples and elms were more abundant than pawpaw in the overstory. However, a wide variety of genera had greater basal area than pawpaws in the overstory, including sweetgum, maple, tulip poplar, oak, blackgum, elm, ash, hackberry, and musclewood.

In order of importance for basal area, the five genera that contributed most greatly to the overstory were sweetgum, maple, tulip poplar, oak, and blackgum. When maples were excluded, the remaining four genera comprised 71% of the total basal area in the overstory. Nevertheless, these four genera contributed only 0.5% of the basal area to the midstory. With regard to relative density, these four genera contributed only 5.5% to the herb layer, 2.3% to the shrub layer, and 0.2% to the midstory stratum. Clearly, changes in relative importance among genera across the lower strata have already begun to filter into the forest community found in the overstory.

DISCUSSION

Our findings suggest that deer may have prevented a broad spectrum of tree species from transitioning above the height at which browsing occurs and into the midstory stratum, thereby preventing regeneration into the overstory. These species include sweetgum, tulip poplar, blackgum, hackberry, and 12 species of oak. Five species of hickory were less commonly encountered in the survey, so their patterns across forest strata were less clear. Nevertheless, the perspective that deer negatively impact a wide range of canopy tree species, including hickory, is well supported (Rooney & Waller 2003; Rossell et al. 2005; Long et al. 2007; Wakeland & Swihart 2009).

The near absence of redbud trees and flowering dogwoods in this forest suggests that, in addition to the negative effects deer have on canopy species, browsing by deer may have limited the success of subcanopy tree species at WWNP. In a past survey of WWNP, Lindsey et al. (1969) noted that musclewood, redbud, and dogwood were common in the overstory, but were not regenerating in the herb layer. In that study, redbud and musclewood both contributed to basal area. In our current study, only mature musclewood trees contributed to basal area, while redbud and flowering dogwood have been all but lost from the forest. Indeed, only 15 musclewood stems occurred in the shrub and midstory strata, even though 53 musclewood trees were found in the overstory.

In contrast to the declines seen for most tree species, pawpaws and maples appear to have increased in abundance. Given that pawpaws comprised 88% of the stems in the shrub layer and 95% of the stems in the midstory stratum, this one species has had phenomenal success in regenerating. Historically, pawpaws were reasonably abundant at WWNP. In their survey, Lindsey et al. (1969) observed pawpaw to be common in the herb layer and very abundant in the shrub layer. However, they did not observe pawpaw as components of the midstory nor overstory. In contrast, we observed near mono-dominant status in the shrub and midstory strata. Slater & Anderson (2014) found a similar response to deer in an Illinois forest. In their case, the density of pawpaw stems nearly doubled in a five-year period, while the density of stems declined for seedlings/saplings of most other species. Given the recent and rapid increase in pawpaws, browsing by deer provides a convincing explanation for the increase in pawpaw abundance and decrease of other species.

Maples also appear to have benefitted from browsing pressure by deer, with maple being the most abundant genus in the overstory. When examined at a species level in the midstory, though, only sugar maple was an important contributor, while boxelder and red maple were not (Table 1). In the survey by Lindsey et al. (1969), sugar maple was only a modest component of trees in the overstory and contributed only 1.3% to basal area. However, sugar maple provided 7.6% of the basal area in the current study. Thus, the success of the maple genus was really due to the exceptional regeneration success of sugar maple over the last 40+ years. Sugar

maple often experiences browsing only when more preferred species are no longer available, leading to it becoming more common in forests browsed by deer (Strole & Anderson 1992; Anderson & Katz 1993; Rooney & Waller 2003; Belden & Pallardy 2009).

While the patterns discussed suggest that deer may be an important influence on diversity at WWNP, other factors have also been tied to the decline in abundance of tree species. Species differences in shade tolerance can cause variation in regeneration success among tree species. For example, tulip poplar is viewed as a shade-intolerant species that requires large gaps or clearings for successful colonization (Orwig & Abrams 1994; Busing 1995; Kota et al. 2007). Similarly, shade intolerance has been argued to play a role in the failure of oak regeneration (Aldrich et al. 2005). Moreover, both pawpaw and sugar maple are considered to be shade tolerant species (Belden & Pallardy 2009; Slater and Anderson 2014). Fire suppression has also been suggested to reduce the regeneration of canopy dominants species in Eastern forests; Abrams & Nowacki (2008) stated that there exists "a direct link between Indian burning and the widespread distribution of mast species." In contrast to oak and hickory species, which would be favored by burning forests, sugar maple is favored in conditions of fire suppression.

This survey of WWNP was not experimental, so the observations generated in the study cannot discriminate among factors to determine which factor(s) caused the current patterns nor can this study demonstrate which influences are responsible for the changes since the survey by Lindsey et al. (1969). Nevertheless, many remnant forests (including WWNP) may be in situations where action is needed, even in the face of this uncertainty. One such action, deer culling, has been practiced at WWNP for more than a decade, based on the presumption that reducing the deer population would improve conditions for trees species other than sugar maples.

Given the putative shade barrier of pawpaw in the shrub and midstory layers, additional management may be needed beyond hunting deer. Pawpaw can be expected to affect the forest community by acting as a recalcitrant layer (Shotola et al. 1992; Shelton et al. 2014; Slater & Anderson 2014). This putative legacy from decades of intensive deer browsing may prevent forest regeneration from maintaining a highly diverse forest at WWNP. Still, this concern of

barriers to regeneration is larger than just this one forest preserve. Given potential plant barriers to regeneration that have been observed for a variety of herbaceous plants and woody species across a range of forest habitats (Tighman 1989; Stromayer & Warren 1997; Goetsch et al. 2011; Tanentzap et al. 2009; Kain et al. 2011; Johnson et al. 2015), this legacy issue may be the primary problem to solve once deer overpopulation concerns have been addressed. The specific problem of pawpaw's expanding range (via sugar maple expansion and mesophication—*sensu* Abrams & Nowacki 2008), combined with continued high deer densities, may make pawpaw the most common recalcitrant layer in old growth forests (Slater & Anderson 2014).

Therefore, we suggest that management actions should take place, and that those actions should incorporate experimental methodology in order to confirm the impact that deer have, both directly through browsing and indirectly by creating a recalcitrant layer. Specifically, we suggest that experimental removal of pawpaw, coupled with protection of vulnerable seedling/sapling species, may be necessary to counter both overabundance due to decades of preferential browsing by deer and the current browsing pressure caused by deer. Such an experiment may also provide valuable information regarding the relative importance of: (a) current deer browsing, (b) constraints associated with canopy tree reestablishment due to pawpaw shading, and (c) the interaction between browsing by deer and shading by pawpaw.

If action is not taken, a wide range of alterations to the forest community can be expected, given the dramatic reduction in the number tree species and concomitant loss of canopy resources. Just from a vegetative structure perspective, deer have been noted to cause the reduction in bird density and diversity by simplifying the understory (Martin et al. 2010; Chollet et al. 2015). However, the greater effect may come from the reduction in tree species. Reduction in oak species, for example, can alter community dynamics in several ways. First, oaks provide resources for 500+ insect species (Marquis & Wheelan 1994; Tallamy 2007), while maples act as host to little more than half that number. Second, shelter-building caterpillars on oaks enhance species richness of other invertebrates (Lill & Marquis 2003). In addition, because abundance and diversity of arthropods is greater on oak trees, greater oak abundance may provide

more food resources for more bird species. Still, population and community dynamics of insectivorous birds in response to oak abundance has remained unexamined. Third, leaf litter composition in woodland ponds can influence amphibian success (Rubbo & Kiesecker 2004). Both frog and salamander species had greater survival when reared in a system that used oak leaf litter versus maple leaf litter. Finally, acorns act as a food resource for many mammals, and acorn production can influence mammalian population growth and density (Jones et al. 1998). Thus, deer may reduce trophic complexity of forest communities by altering community structure and composition through selective herbivory (Rooney & Waller 2003), and the effect of deer may be even more exacerbated by their indirect suppression of tree reestablishment if they indirectly create recalcitrant layers.

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