RESEARCH PAPER

White-tailed deer herbivory impacts on tree seedling and sapling abundance in the Lake States Region of the USA

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Abstract

Key message **White-tailed deer (*Odocoileus virginiana* Zimmermann) browsing reduces seedling and sapling abundance of more palatable winter woody browse such as *Tsuga canadensis* L. Carrière, *Thuja occidentalis* L., *Betula alleghaniensis* Britton, and *Pinus strobus* L. across the Lake States Region of the USA.**

Context White-tailed deer consume buds and twigs of tree seedlings and saplings as forage. Deer populations in the Lake States Region of the USA have increased over recent decades due to a decrease in predators and an increase in habitat fragmentation. Higher deer population densities present challenges to regeneration of tree species.

Aims The objective of this work was to quantify the effects of deer browsing on tree seedling and sapling abundance and species richness of woody tree species which vary in deer browse palatability.

Methods Deer browsing impact measurements from the tree regeneration indicator from the US Department of Agriculture Forest Service's Forest Inventory and Analysis program were used to predict seedling and sapling abundance from overstory basal area and a deer browsing index in the Lake States Region.

Results Overstory basal area was important in predicting seedling and sapling abundance for all species ($p < 0.05$). Deer browsing affected seedling and sapling abundance differently across species, with the most palatable species showing lower stocking or negligible effects with browse.

Conclusion Results support the importance of quantifying impacts of deer browsing for use in determining the survival and abundance of palatable species in the smallest size cohorts.

Keywords Ungulate browsing · Forestry · Forest inventory and analysis program · Regeneration

1 Introduction

The ecological effects of white-tailed deer (*Odocoileus virginianus* Zimmerman) have been studied frequently, due to their overabundance – existing in greater abundance than the ecosystem can sustain – in many regions such as across the Northern United States (US; i.e. (Anderson and Loucks 1979; Alverson et al. 1988; Waller and Alverson 1997;

Cornett et al. 2000; Ripple et al. 2010; Bradshaw and Waller 2016; Miller and McGill 2019). Human expansion, urbanization, and conversion to agriculture have largely pushed predators out of deer ranges. The fragmented landscape creates forest edges and gaps providing ideal habitat for deer. A historical effort to increase game populations and decrease predator populations (e.g., wolves, *Canis lupus*, Lewis and Murray 1993) has created a unique niche for white-tailed deer across the US Lake States. White-tailed deer primarily consume herbaceous vegetation during the growing season and the buds and twigs of palatable trees during the winter months (Rogers et al. 1981; Anderson et al. 2002). Once the terminal buds of trees grow beyond deer browsing height (~ 2.1-m tall), the severity of browsing is decreased, which makes seedlings and saplings the most vulnerable to damage and death (Anderson et al. 2002; Bradshaw and Waller 2016; Ramirez et al. 2019). Suppression of tree species in these early stages of growth can alter the forest composition for

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decades (Anderson and Loucks 1979; Alverson et al. 1988; Frerker et al. 2014).

White-tailed deer are selective herbivores and will browse "preferred" tree species (Rawinski 2014). Selective browsing by ungulates can cause a reduction in regeneration success of desired tree species and/or an increase in abundance of non-palatable species by reducing competition (Côté et al. 2004; Russell et al. 2017a). In the US Lake States Region, eastern hemlock (*Tsuga canadensis* [L.] Carrière), northern white cedar (*Thuja occidentalis* L.), yellow birch (*Betula alleghaniensis* Britton), northern red oak (*Quercus rubra* L.), and eastern white pine (*Pinus strobus* L.) are all highly palatable species for deer (Dahlberg and Guettinger 1956; Bradshaw and Waller 2016). Frelich and Lorimer (1985) identified white-tailed deer as a major cause of *T. canadensis* decline in the Porcupine Mountains of the Upper Peninsula of Michigan and predicted a long-term decline in *T. canadensis*. In mixed *Acer saccharum* Marshall-*T. canadensis* forests, overbrowsed *T. canadensis* seedlings and saplings cannot resprout as vigorously as their competitors, which limits recruitment into the mid- and overstory (Switzenberg et al. 1955; Anderson and Loucks 1979; Salk et al. 2011). *T. occidentalis*, which is also a slow growing, long-lived conifer, can survive in a suppressed state for many years. When browsed by deer, *T. occidentalis* can be outcompeted by other non-palatable species such as balsam fir (*Abies balsamea* [L.] Mill.), causing a decline in the recruitment of young *T. occidentalis* (Cornett et al. 2000). In both examples, deer browsing resulted in a competitive advantage for non-preferred browse species, shifting the species composition of these forests (Palik et al. 2015).

Indirect effects of deer herbivory on the forest ecosystem include changes in the food web, vegetation structure, and nutrient cycling (Rooney and Waller 2003; Nuttle et al. 2014; Ramirez et al. 2018, 2021). Long-term data collection and complex herbivory effects limit the frequency and feasibility of studying indirect browse response on the landscape. However, models have been developed which show that deer can cause ecosystem-wide changes through cascading effects on soil structure and nutrients, mammalian and avian communities, and invertebrate diversity (DeCalesta 1994; Waller and Alverson 1997; Royo and Carson 2006; Ramirez et al. 2021).

Deer populations in the US Lake States have increased in recent decades, making them overabundant in some areas and a threat to regenerating tree species (Rooney and Waller 2003; Ripple et al. 2010; Patton et al. 2018; Miller and McGill 2019). When quantifying deer herbivory relationships, deer density is as important as understanding forest stand and site attributes in the development of forest understories (Russell et al. 2017b). Precise deer population measurements are difficult to estimate, especially consistently across land ownership and state boundaries. Additionally,

deer density numbers may not reflect deer browse impact, which is non-linear and depends on the carrying capacity of the ecosystem (Keyser et al. 2006; Lesser et al. 2019; Ramirez et al. 2021). To begin to systematically quantify impacts of deer browsing, the US Department of Agriculture (USDA) Forest Service's Forest Inventory and Analysis (FIA) program has implemented a protocol to provide a site-specific estimate of deer browse pressure through "browse scores" at each FIA plot (McWilliams et al. 2015). This method provides a regionally consistent metric to assess the impacts of deer browsing on tree regeneration across large areas. We define deer browse impact as a negative impact to woody seedlings and saplings from browse. The scope of many deer herbivory studies has been limited to small exclosure (e.g., (Cornett et al. 2000; White 2012; Waller and Maas 2013; Frerker et al. 2014; Shelton et al. 2014)) or enclosure studies (Horsley et al. 2003; Nuttle et al. 2014), which are important for determining effects of species at local scales, but restricted by extent. There is a need for more landscape or regional studies of deer browsing impacts (Russell et al. 2017a, b; Lesser et al. 2019).

Our study aims to examine the effects of white-tailed deer browsing on the smallest cohorts of trees in US Lake States forests, using the FIA browse impact measurements. Specific objectives are to (1) quantify effects of browsing on species diversity of seedlings and saplings at the plot level and (2) model the effects of deer browse presence on seedling and sapling abundance for some of the most common species in the Lake States across a range of browse palatability.

2 Materials and methods

2.1 Study area

This study was conducted in the Lake States Region of the USA in the states of Michigan (MI), Minnesota (MN), and Wisconsin (WI). The Lake States Region contains diverse forest types and are comparable to many of the world's forests found in cool-to-cold temperate zones (Frelich 2002). The landscape in the Lake States contains a mixture of tallgrass prairie, temperate deciduous forests, and mixed boreal forest biomes (Albert 1995). Historically, wind and fire have influenced the forest composition with land clearing beginning around 1880. The growing season extends from approximately late April to early October with average summer temperatures between 23 and 27 °C and average winter low temperatures between − 20 and − 7 °C. Areas within 10 km of the Great Lakes experience a strong lake effect creating higher temperatures in the winter and lower temperatures in the summer. Precipitation occurs mostly in the growing season with 800 to 900

mm annually. Estimated deer density in this region varies from 0 to 30 per square kilometer (Adams et al. 2009; Bradshaw and Waller 2016).

2.2 Forest inventory and analysis data

The USDA Forest Service's FIA program was the primary source of forest inventory data for this project. The FIA protocols are nationally consistent and provide a basis for comparison across regions of the USA (Bechtold and Patterson 2005). This analysis utilized forest stocking information from permanent plots, termed phase 2 (P2) plots; there is approximately one P2 plot in every 2428 ha of forested land. FIA data was subset to single condition forested plots from the most recent measurement cycle, which is 5 years in Minnesota and 7 years in Michigan and Wisconsin to obtain full sampling coverage from each state without duplication. Additional data on ungulate browse were obtained from phase 2-plus (P2-plus) plots, which were developed and implemented in 2012 in the Northern US on a subset of P2 plots (McWilliams et al. 2015). On P2-plus plots, deer browse impact was recorded and defined as consumption of shoots, twigs, and leaves by animals, typically ungulates, for food and was categorized on a scale of 1 through 5 (within an exclosure, no browse, low browse, high browse, and severe browse, respectively) on seedlings at least 5.08 cm tall. Plots with a browse score of 1 were removed for a total of 768 P2-plus plots used in this analysis.

All FIA data were accessed via the "FIA DataMart" (https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv. html, downloaded 13 June 2020). From the P2 FIA plots, the CONDITION, PLOT, TREE, and SEEDLING tables were used to obtain information on live trees. Tree-level variables such as diameter at breast height (DIA), tree height (HT), unadjusted trees per acre (TPA_UNADJ), species identification (SPCD), and deer browse impact score (BROWSE_IMPACT) were utilized to summarize tree data for this analysis. Additional information on inventory sampling and data processing is well-documented in Bechtold and Patterson (2005). The definition of overstory trees and saplings was ≥ 12.45 cm and 2.54 to 12.45 cm DBH (diameter at breast height, 1.4 m, from ground), respectively. Tree seedlings were defined as at least 15.2 and 30.5 cm in height for conifers and hardwoods, respectively, with both having a DBH ≤ 2.54 cm. Basal area per hectare (BA m^{2}ha^{-1}) was summarized for each plot by size class (overstory trees or saplings). Trees per hectare (TPH) was summarized for each plot for all size classes. From the P2-plus FIA plots, the PLOT_REGEN tables were used to obtain information on browse impact.

2.3 Study species

Bradshaw and Waller (2016) classified ten common Wisconsin tree species into palatability classes ranging from least to most palatable based on previous studies from the region (Dahlberg and Guettinger 1956; Frerker et al. 2014) in combination with 25 years of expertise on deer impacts. The five species chosen as most palatable in this analysis were assigned a high rating on the Bradshaw and Waller (2016) palatability scale and included *T. canadensis*, *T. occidentalis*, *B. alleghaniensis*, *Q. rubra*, and *P. strobus*, hereafter referred to as the palatable species. Five less palatable included were *Abies balsamea*, *Picea* spp. (*P. glauca* [Moench] Voss and *P. mariana* (Mill.) Britton, Sterns & Poggenb.), *Acer rubrum* L., *Acer saccharum*, and *Populus tremuloides* Michx, hereafter referred to as the unpalatable species.

2.4 Analysis

All analyses occurred at the plot level. Tree stand and stocking information were summarized using FIA data to provide TPH for seedlings, saplings, and overstory trees and overstory BA by species at the plot level. Seedling and sapling species richness, Shannon's diversity index, and Simpson's diversity index were compared by browse score using a one-way ANOVA and Tukey honest significant differences (HSD) post hoc analyses for significant differences. Browse scores of 4 and 5 were combined into a high/severe category, as there were only two plots identified with severe browse in this dataset.

Generalized linear models (GLM) were fit to predict individual species seedling and sapling abundance (TPH) as a function of overstory basal area and deer browse impact. Poisson and negative binomial count distributions were fit to the GLMs, and ultimately, Poisson models were utilized in the analysis. Models were fit for each of the ten target species and all species found on a plot. Browse impact and species-specific overstory BA were used as predictors for individual species models. A dummy variable (0,1) was created to describe two levels of deer browse: none (browse score 2) and browse present (browse score 3, 4, or 5). If a predictor was not significant (i.e., $p > 0.05$), it was removed from the model to minimize overfitting. R computational software was utilized in creating statistical models (R Core Team 2015):

$$TPH = e^{b0 + b1*browseIndicator + b2*overstoryBA} \qquad (1)$$

where *TPH* is trees per hectare of either seedlings or saplings of target species, *overstoryBA* is the overstory basal area (m^{2}ha^{-1}) of target species, and *browseIndicator* is deer

Fig. 1 Distribution of study
species across the Lake States.
Black dots indicate plots where
at least one seedling, sapling,
or overstory tree of that species
was recorded on a FIA P2 plot
within the most recent data
cycle. Gray dots indicate a
subset of plots that were also
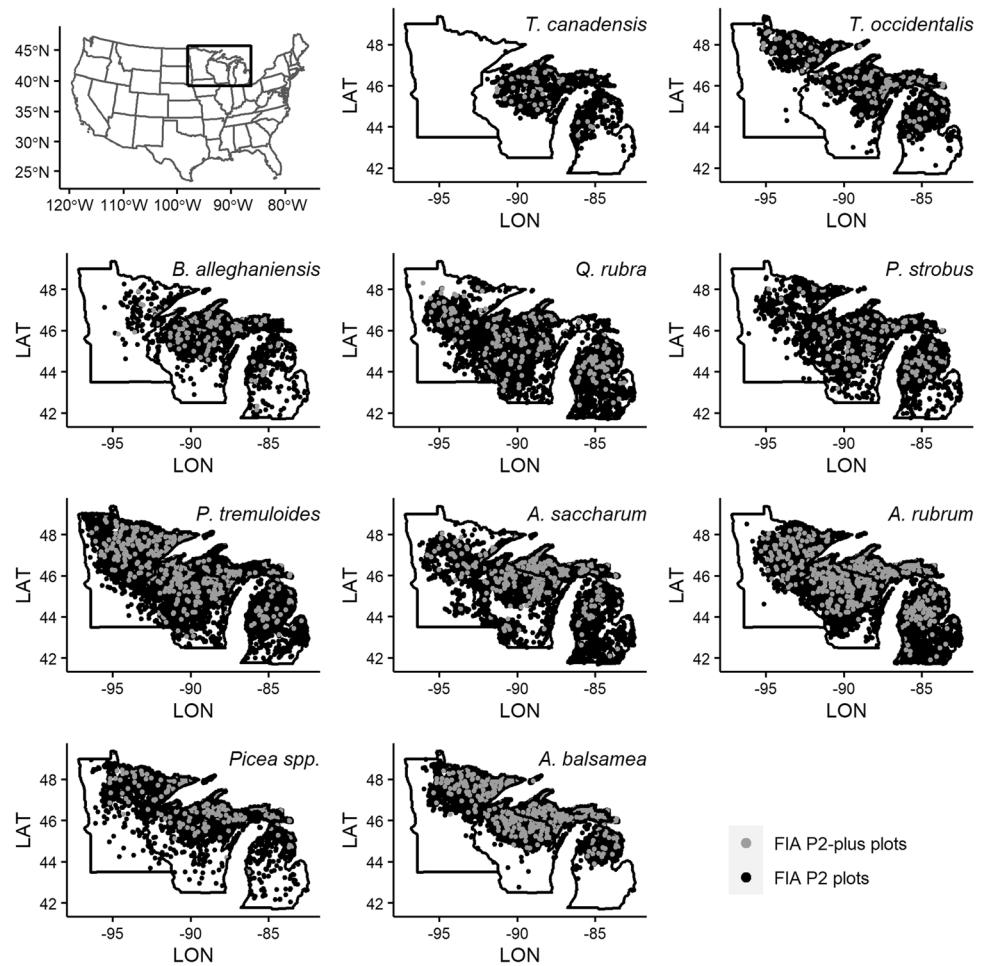assigned a browse score from
FIA P2-plus plots

Fig. 2 Number of plots contain-
ing at least one seedling or sap-
ling of the target 10 species for
all FIA P2-plus plots from the
most recent measurement cycle.
Species are sorted from most
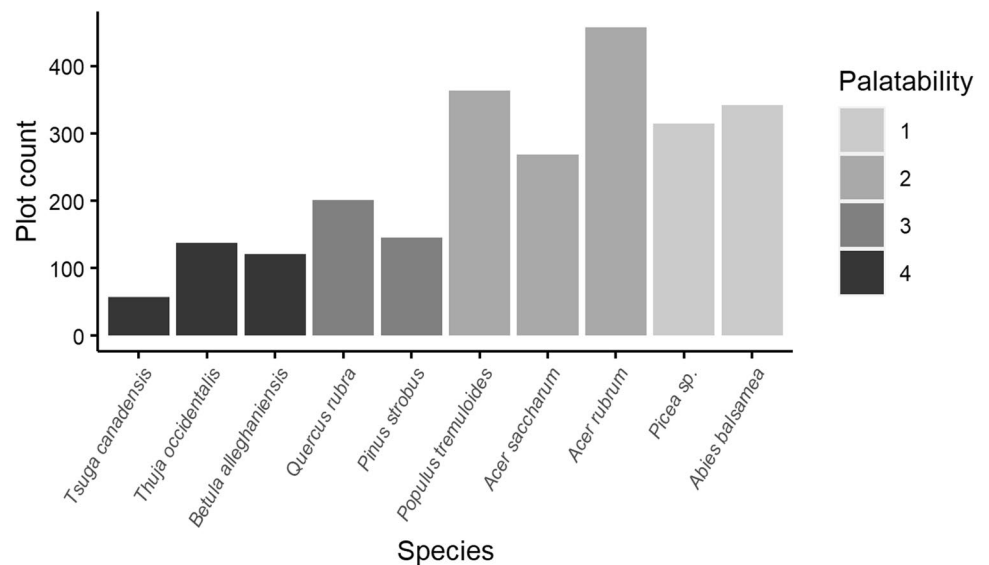(4) to least (1) palatable for deer
browsing from left to right

Table 1 Summary statistics for abundance of each species and all species on P2-plus FIA plots from the most recent cycle of data ($n = 768$)

Species	Prop 0s[1]	Plots	Minimum	Mean	Maximum	Standard deviation
Overstory			Trees per hectare			
All species	0.03	748	3.7	117.2	478.6	69.8
T. canadensis	0.16	48	3.7	20.3	101.0	26.1
T. occidentalis	0.07	128	3.7	81.3	437.5	88.0
B. alleghaniensis	0.16	102	3.7	11.4	74.8	11.7
Q. rubra	0.41	118	3.7	17.1	86.0	16.5
P. strobus	0.26	108	3.7	19.3	157.1	25.8
P. tremuloides	0.17	303	3.7	33.1	205.7	40.0
A. saccharum	0.21	213	3.7	38.9	142.1	32.3
A. rubrum	0.29	325	3.7	24.2	149.6	22.8
Picea spp.	0.33	103	3.7	11.7	145.8	18.3
A. balsamea	0.23	263	3.7	23.3	115.9	22.5
Saplings			Trees per hectare			
All species	0.09	701	46.6	422.2	3121.0	375.7
T. canadensis	0.79	12	46.6	77.6	232.9	53.8
T. occidentalis	0.63	51	46.6	227.4	978.2	232.8
B. alleghaniensis	0.74	31	46.6	84.1	372.7	70.6
Q. rubra	0.82	36	46.6	81.5	326.1	61.4
P. strobus	0.75	36	46.6	151.4	885.0	202.7
P. tremuloides	0.59	150	46.6	322.7	2515.4	397.6
A. saccharum	0.48	140	46.6	139.1	652.1	111.6
A. rubrum	0.61	180	46.6	136.6	698.7	127.5
Picea spp.	0.76	37	46.6	88.1	652.1	104.0
A. balsamea	0.38	212	46.6	234.2	1257.7	229.1
Seedlings			Trees per hectare			
All species	0.03	748	46.6	2138.2	11645.3	1945.5
T. canadensis	0.54	26	46.6	157.7	652.1	175.3
T. occidentalis	0.54	63	46.6	704.6	5170.5	996.8
B. alleghaniensis	0.65	42	46.6	208.5	2096.2	358.2
Q. rubra	0.35	131	46.6	174.9	1956.4	228.5
P. strobus	0.39	88	46.6	267.3	2142.7	389.9
P. tremuloides	0.44	203	46.6	585.1	6428.2	1140.0
A. saccharum	0.22	210	46.6	1174.3	10341.1	1854.6
A. rubrum	0.31	317	46.6	506.7	4937.6	705.7
Picea spp.	0.48	80	46.6	137.4	838.5	148.6
A. balsamea	0.17	283	46.6	463.5	6241.9	633.6

[1]Prop 0s indicates the proportion of plots with 0 trees on a plot recorded of the respective size class and species

Statistics calculated for plots when defined species was present on a plot

browse impact indicator (0 for no browse, 1 for browse present).

3 Results

The five most palatable deer browse species used in this analysis displayed different geographic distributions across the Lake States but represent their respective natural ranges (Fig. 1). *T. canadensis* did not occur on P2 plots within Minnesota but was recorded in Wisconsin and Michigan. *T. occidentalis* occurred across the northeast region of the Lake States. The majority of *B. alleghaniensis* observations occurred in northern Wisconsin and the Upper Peninsula of Michigan, with scattered individuals in the Lower Peninsula of Michigan and the northeast region of Minnesota.

There were generally fewer plots containing the highest palatable deer browse species (*T. canadensis*, *T. occidentalis*, *B. alleghaniensis*, *Q. rubra*, *P. strobus*) compared to the less palatable species (*P. tremuloides*, *A. saccharum*, *A.*
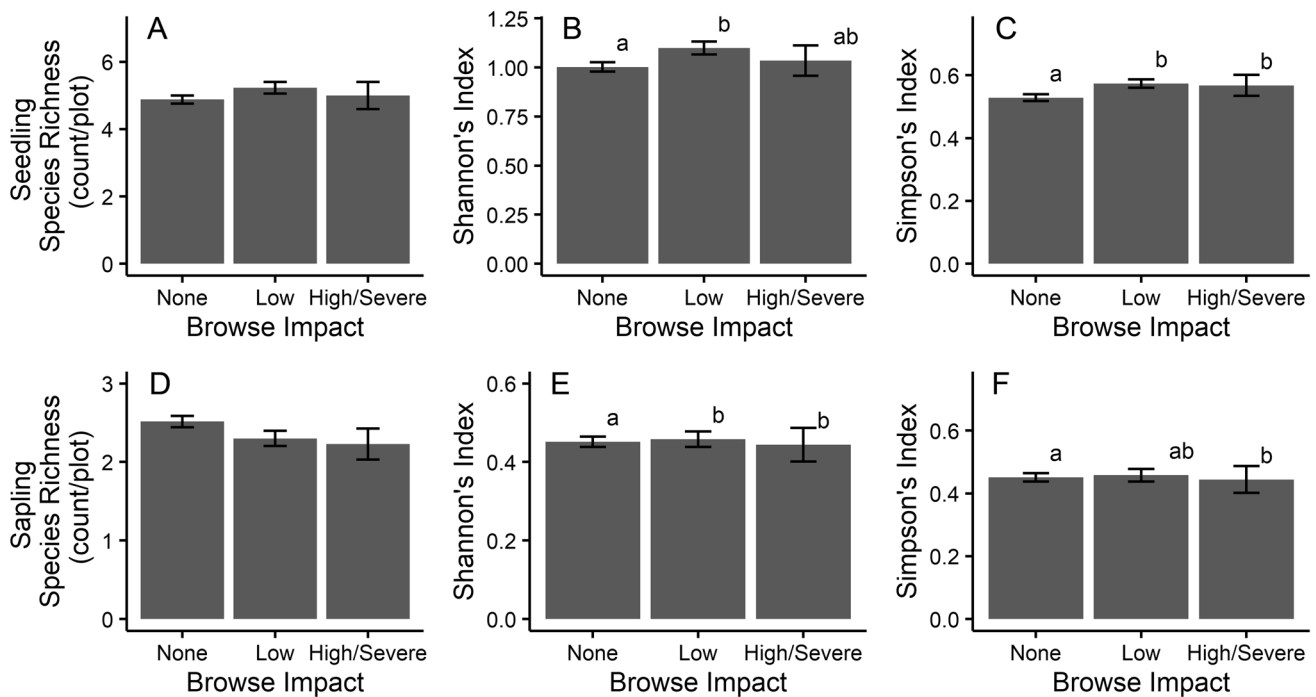
Fig. 3 Species richness, Shannon's diversity index, and Simpson's diversity index for seedlings (A, B, C, respectively) and saplings (D, E, F, respectively) for all FIA P2-plus plots from the most recent measurement cycle by browse level. Browse impact high and severe are combined. Error bars represent ± 1 SE. Lowercase letters denote significant differences between deer browse impacts (ANOVA, $p < 0.05$)

rubrum, *Picea* spp., *A. balsamea*; Fig. 2). Of plots containing at least one tree of any size class in a particular species, a large proportion of plots had zero individuals in seedling and sapling size classes, the latter being more common (Table 1).

Of the three species diversity metrics calculated, species richness did not reveal any significant differences between browse levels. Shannon's diversity index showed a significant increase in seedling and sapling abundance with browse presence of "low" compared to "none". Simpson's diversity index showed a significant increase in seedling abundance with "low" browse, but no increase in sapling abundance until the "high/severe" browse category (Fig. 3).

The GLM models for seedling or sapling abundance predicted an increase in seedlings or saplings with an increase in conspecific overstory basal area for most species except *B. alleghaniensis*, *Q. rubra*, *P. tremuloides*, and *A. rubrum* for seedlings and *B. alleghaniensis* and *Q. rubra* for saplings (Table 2, Figs 4 and 5). All species combined predictions for seedlings and saplings showed a slight decrease in the respective understory abundance, with increasing overstory basal area. For *T. canadensis* and *A. balsamea* saplings, browse presence was not a significant predictor ($p > 0.05$) and was therefore removed from the model. Where browse presence was significant, browse presence was predicted to decrease the seedling abundance for *T. canadensis*, *T. occidentalis*, *B. alleghaniensis*, *P. strobus*, *P. tremuloides*,

A. saccharum, and all seedlings combined. Likewise, a decrease in sapling abundance with browse presence was predicted with *T. occidentalis*, *B. alleghaniensis*, *Q. rubra*, *P. strobus*, *P. tremuloides*, *A. saccharum*, and with all saplings combined.

4 Discussion

This study provides an estimate of the regional impacts of deer browsing on reducing palatable woody species abundance in seedlings and saplings. Given the known cascading effects of deer browse on other trophic levels (e.g., Churski et al. 2017; Côté et al. 2004; Ripple et al. 2010; Miller and McGill 2019; Ramirez et al. 2021), this analysis provides a baseline for long-term predicted effects of deer browse on commercially and ecologically important species in the US Lake States. This analysis leverages data across the Lake States Region to quantify the effects of deer browsing on small cohorts of trees and contrasts these effects between several species that vary in deer browse palatability.

Long-term deer browsing can cause reduced species richness of herbaceous and woody species within forested landscapes (Anderson and Loucks 1979; Frelich and Lorimer 1985; Waller and Alverson 1997; Russell et al. 2001). Herbivore overabundance is site-specific; therefore, there may

Table 2 Model fit parameters and statistics for seedling and sapling models

Species	b_0	b_1	b_2	RMSE	AIC
Seedlings					
All species	7.718	− 0.003	− 0.073	1948.71	1231567
T. canadensis	4.290	− 0.713	0.051	132.95	9179
T. occidentalis	5.525	− 0.621	0.030	746.17	124036
B. alleghaniensis	4.966	− 0.846	− 0.197	231.76	28616
Q. rubra	4.801	0.032	− 0.020	203.58	41834
P. strobus	5.063	− 0.261	0.032	329.10	54675
P. tremuloides	6.245	− 0.830	− 0.052	898.53	355937
A. saccharum	6.255	− 0.266	0.075	1536.97	410471
A. rubrum	5.869	0.229	− 0.034	634.52	316523
Picea spp.	4.237	0.167	0.025	129.68	22132
A. balsamea	5.664	0.212	0.104	598.78	194178
Saplings					
All species	6.325	− 0.016	− 0.208	369.00	246407
T. canadensis	2.537	NA	0.041	39.55	3172
T. occidentalis	4.068	− 0.176	0.030	176.56	30773
B. alleghaniensis	3.500	− 0.912	− 0.038	50.41	8062
Q. rubra	2.983	− 0.415	− 0.047	40.48	11309
P. strobus	3.783	− 0.790	0.031	118.50	20303
P. tremuloides	4.977	− 0.449	0.014	299.09	137483
A. saccharum	4.131	− 0.111	0.028	105.40	35297
A. rubrum	3.820	0.288	0.010	103.89	63213
Picea spp.	2.427	0.513	0.199	56.04	9327
A. balsamea	4.646	NA	0.152	206.41	79260

Parameters b_0, b_1, and b_2 were fit with Eq. 1. Model performance criteria include RMSE (root mean square error) and AIC (Akaike information criterion)

be regions where deer populations are high and available browse is abundant, causing less impact on the forested community. In contrast, lower deer populations may be considered overabundant at sites where available food source is low especially in the winter, causing local extirpation of palatable species. This phenomenon is illustrated through both modeling (e.g., Lesser et al. 2019) and exclosure studies (e.g. Frerker et al. 2014), where shifts in vegetative communities are driven by deer browsing. Our results do not indicate an overwhelming decrease in woody species diversity with increasing browse pressure (Fig. 2), but a drop in local plot-level diversity may be expected beyond which deer herbivory leads to local extirpation. In addition, overall plot diversity may not decrease immediately, but a more detrimental shift in which species are present is likely with more severe deer browsing. Our results support the latter theory, as some non-palatable species showed a greater abundance in seedlings or saplings (e.g., *A. rubrum* and *Picea* spp.), a phenomenon not observed at all with the palatable species.

Total seedling abundance was generally lower when deer browse was present across the range of conspecific overstory basal area for the most palatable tree species. (Fig. 4). In our models, overstory BA functioned as a proxy for seed source abundance, reflecting approximate tree regeneration potential, understanding that this does not account for nearby seed source dispersal or seed bank input. At the individual species level, this suggests that selective deer browsing reduces *T. canadensis*, *T. occidentalis*, *B. alleghaniensis*, *P. strobus*, and *P. tremuloides* seedling regeneration in areas where natural regeneration would otherwise be expected – a relationship observed in other studies on seedling abundance (e.g., Anderson and Loucks 1979; Bradshaw and Waller 2016; Côté et al. 2004; Lesser et al. 2019). As an example, we can assume the average basal area of *T. canadensis* overstory trees (20.3 m²), where *T. canadensis* is present, represents an average community for that species. The predicted change in seedling abundance is from 206.4 TPH without browse and 101.1 TPH with browse, greatly reducing the potential of this species to establish in a community where tree regeneration is possible (Fig. 4). In contrast, the three least palatable species, *A. rubrum*, *Picea* spp., and *A. balsamea*, showed a minor increase in seedling TPH with deer browsing, suggesting that these trees may be utilizing the growing space opened from deer browsing to increase abundance.

The effects of browse on *Q. rubra* seedling abundance are statistically significant, but to such a small degree that would not be biologically significant. *Q. rubra* are well-adapted to fire disturbance, which has reduced recruitment of many *Quercus* species with recent decades of fire suppression (Abrams 1992; Nowacki and Abrams 2008). Mesophication – transitioning to a mesic environment due to fire suppression that stimulates less fire-susceptible communities – has been associated with oak and pine recruitment decline in the Eastern US (Nowacki and Abrams 2008; Hanberry et al. 2020). At the regional scale, these regeneration influences may outweigh effects of deer browse.

In both the seedling and sapling size classes, *B. alleghaniensis* and *Q. rubra* showed a decrease in TPH with increasing overstory BA, somewhat contrary to what you might expect if overstory BA is a proxy for seed source availability. While *B. alleghaniensis* seeds are dispersed by wind and may be plentiful in heavy seed years, without available light seedlings will not likely survive. This also may be attributed to the fact that *B. alleghaniensis* is rarely found in pure stands but is often a component of mixed species stands that are frequently managed for uneven-aged stand structures. For one of the most palatable species examined in this study, *B. alleghaniensis* displayed the lowest mean number of overstory trees relative to other species, reflecting its lower abundance compared to other browse-sensitive species in the region (Table 1). For *Q. rubra*, interspecific competition is a major limiting agent for to successfully establish in sites where a viable seed source is present.
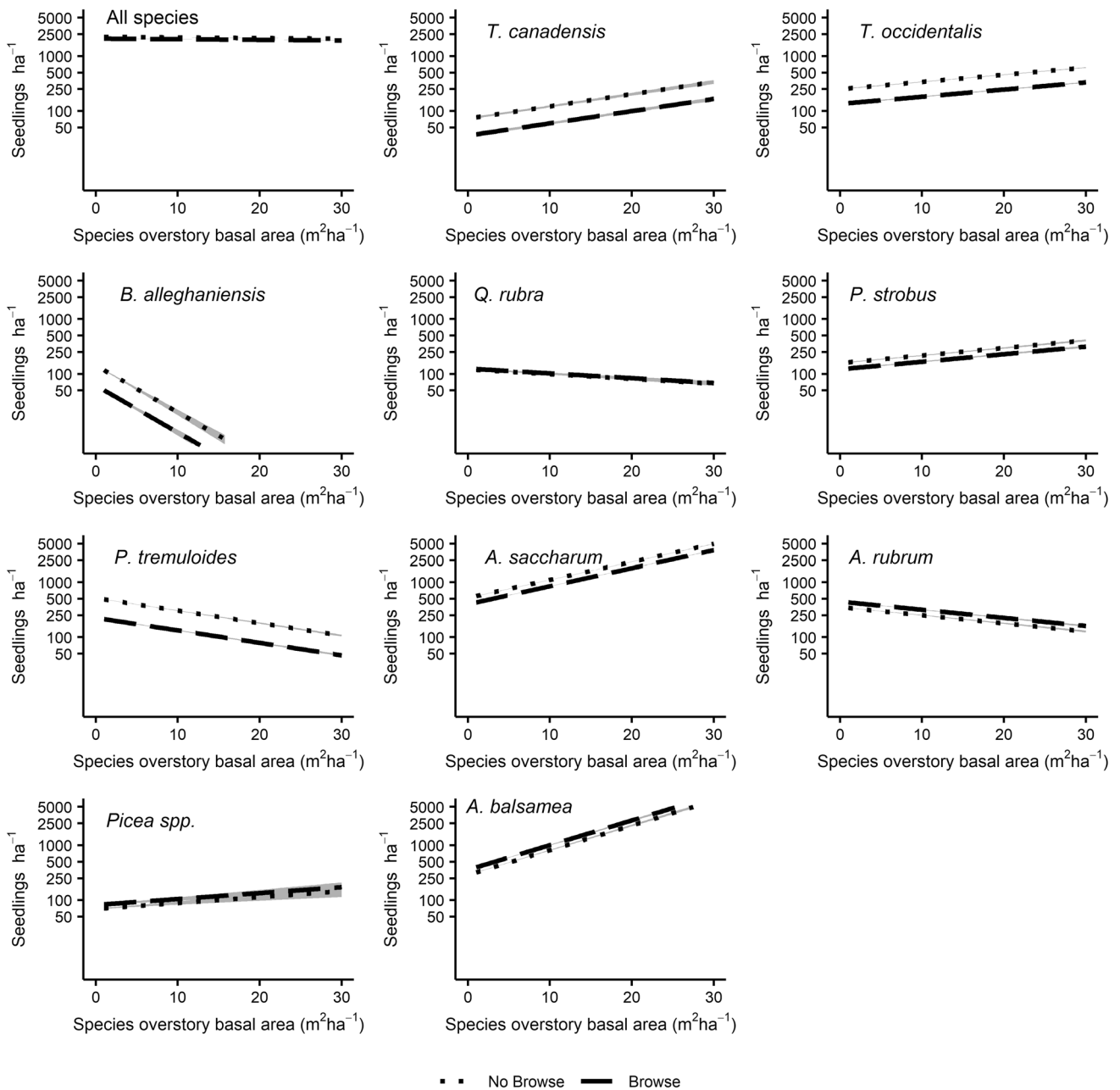
Fig. 4 Predicted seedlings per hectare by overstory basal area and browse impact for study species in the US Lake States for all FIA P2-plus plots containing seedling and overstory individuals of each respective species from the most recent measurement cycle. Insignificant browse represented by a solid line. 95% confidence intervals represented by gray bands

In the sapling size class, overall abundance was relatively stable or decreasing for all species except *Picea* spp. and *A. balsamea*, illustrating how competition in the overstory limits resources available for individuals in the mid- and understory (Fig. 5). *Picea* spp. and *A. balsamea* are unpalatable deer browse species and highly shade tolerant. *T. occidentalis*, *B. alleghaniensis*, *Q. rubra*, *P. strobus*, *P. tremuloides* and all species combined sapling abundance were all predicted to decrease with deer browse, suggesting small

saplings of these species cannot survive as well under high deer browse or these species were heavily browsed as seedlings, resulting in a reduction in abundance at the sapling size class. *T. canadensis* is the most palatable deer browse species but did not show a statistically significant difference with deer browse in the sapling size class. There are a very small number of plots with *T. canadensis* saplings ($n = 12$), the smallest of any group in this analysis. While the model did not predict a significant difference in sapling abundance
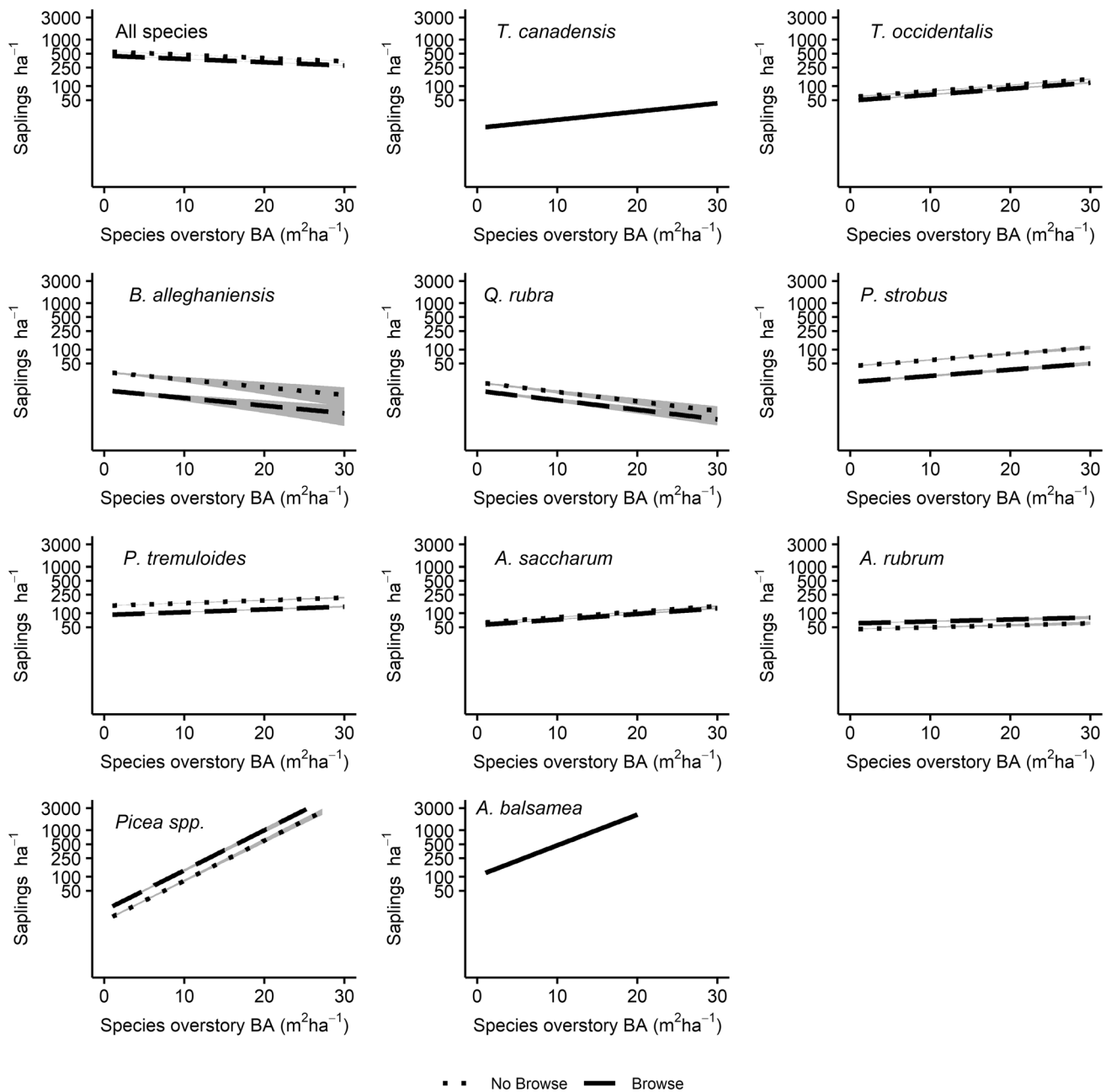
Fig. 5 Predicted saplings per hectare by overstory basal area and browse impact for study species in the US Lake States for all FIA P2-plus plots containing sapling and overstory individuals of each respective species from the most recent measurement cycle. Insignificant browse represented by a solid line. 95% confidence intervals represented by gray bands

with browse, the very small number of plots containing saplings suggests that seedlings may not be surviving long enough to grow into the sapling size class due to browse or other stand dynamics.

Slow growing, long-lived palatable species such as *T. occidentalis* can survive decades within the understory under moderate to intense deer browsing. These species will allocate limited resources to diameter growth until a canopy gap allows suppressed trees to establish in the overstory.

This delay in recruitment is common where *T. occidentalis* is present (Boulfroy et al. 2012). The USDA Forest Service recommends a height of 3 m before *T. occidentalis* is considered out of deer browse range, which can account for 20 to 40 years of growth (Boulfroy et al. 2012). This unique growing strategy may suggest why sapling abundance of *T. occidentalis* is about the same at both levels of browse. At this size class, these trees have grown tall enough to avoid

browse from deer, while other species in the same community are being browsed more heavily.

Models of seedling and sapling abundance were only created for plots that have recorded browse with seedlings or saplings present; therefore, it was difficult to determine if an absence of seedlings or saplings is due to absence of seed source or severe overbrowsing to local extinction. The effects of local browse changes in forest composition may be apparent with additional years of forest inventory and browse score measurements. Additionally, other stressors such as climate change are potentially affecting regeneration of many species due to drier, warmer conditions, especially those that occur at their southern range or on marginal sites, which is not accounted for in this analysis (Salk et al. 2011). Furthermore, high deer densities lead to a greater number of introduced plant species in many of the forest types examined here (Russell et al. 2017a). Hence, deer can indirectly affect seedling and sapling abundance through promoting undesirable vegetation such as invasive plants.

The current abundance of seedlings and saplings represents the effects of past deer populations and may not reflect current deer browse pressure if it differs. The FIA P2-plus dataset, established in 2012, provides deer browse impacts of current and recent years only. In the Lake States, there has been deer overabundance and high browse pressure in some areas for decades (Bradshaw and Waller 2016). The current state of the forest today is the legacy of these recent decades of browse; hence, the current browse score may not capture the long-term impacts of deer browse. Bradshaw and Waller (2016) utilized a browse metric for 10 years prior to the forest inventory data to account for this delay in browse effects. Continual monitoring of deer browse pressure in a nationally consistent manner, which can be accomplished with subsequent remeasurements of the FIA data used here, is necessary to assess deer browse legacy effects on current forest conditions across diverse forest types.

5 Conclusion

Deer can alter the natural succession of forests by severely browsing and potentially eliminating palatable woody and herbaceous species (Waller and Alverson 1997). Regenerating tree species are stressed to find nutrients, light, and space to germinate and then grow into the mid- and overstory. Ungulate browsing provides an additional stressor that alters the natural competition between species and favors some over others, potentially changing the stand dynamics or altering the potential to produce palatable species for economic value. This analysis quantifies the magnitude of the effect of deer browsing across ten common tree species in the Lake States Region, highlighting the importance of considering deer browsing when managing forests for regeneration and considering other cascading effects of deer browsing on the ecosystem.

Declarations

Consent for publication All authors give their informed consent to this publication and its content.

Conflict of interest The authors declare no competing interests.

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