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ARTICLE

Modeling browse impacts on sapling and tree recruitment across forests in the northern United States

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Abstract: Understanding the patterns of tree recruitment is essential to quantifying the future health and productivity of forest ecosystems. Using national forest inventory information, we incorporated browse impact measurements into models of sapling (2.5–12.7 cm diameter at breast height (DBH)) and overstory tree (≥12.7 cm DBH) ingrowth across the northern United States. Ingrowth was modeled with standard and zero-inflated techniques using discrete Poisson and negative binomial distributions. Zero-inflated models using stand attributes and browse impacts provided the best fit statistics for modeling the occurrence and frequency of ingrowth over a 5-year time period. Results indicate that stands with very high browse impact would contain 50.0% fewer ingrowth saplings compared with stands with no browse impact. Greater browse impacts similarly yielded a negative effect on overstory tree ingrowth, but to a lesser degree than saplings. Despite the stochastic nature of ingrowth observations, incorporating browse impacts may be essential in determining accurate levels of ingrowth in forests where herbivory constrains forest regeneration objectives.

Key words: herbivory, white-tailed deer, regeneration, ingrowth, Forest Inventory and Analysis.

Résumé : Il est essentiel de comprendre les patrons de recrutement des arbres pour quantifier l'état de santé et la productivité futures des écosystèmes forestiers. À partir des informations tirées de l'inventaire forestier national, nous avons incorporé des mesures d'impact du broutage dans des modèles de recrutement des gaules (2,5–12,7 cm de diamètre à hauteur de poitrine (DHP)) et des tiges (≥12,7 cm au DHP) dans l'étage dominant à travers le nord des États-Unis. Le recrutement a été modélisé à l'aide de techniques standards et avec une surreprésentation de zéros en utilisant les distributions de Poisson et binomiale négative. Les modèles avec une surreprésentation de zéros utilisant les attributs du peuplement et les impacts du broutage fournissaient les statistiques les mieux ajustées pour modéliser l'occurrence et la fréquence du recrutement sur une période de 5 ans. Les résultats indiquent que les peuplements sévèrement impactés par le broutage contiendraient 50,0 % moins de recrues comparativement aux peuplements exempts de broutage. Des impacts plus importants dus au broutage ont de façon similaire eu un effet négatif sur le recrutement des tiges dans l'étage dominant, mais à un degré moindre que dans le cas des gaules. Malgré la nature stochastique des observations au sujet du recrutement, l'introduction des impacts du broutage peut s'avérer essentiel pour déterminer le degré exact de recrutement dans les forêts où le broutage menace les objectifs de régénération forestière. [Traduit par la Rédaction]

Mots-clés : broutage, cerf de Virginie, régénération, recrutement, Analyse et Inventaire Forestier.

Introduction

Tree recruitment is the accretion of newly established trees of a certain size in forest stands. Quantifying tree recruitment is essential to forest managers and is an integral component of forest growth and yield models. Dynamic approaches to modeling recruitment include specifying parameters that are sensitive to stand conditions such as density and composition (Weiskittel et al. 2011*a*). Through remeasurement of permanent sample plots, ingrowth can be defined as trees that grow into a specified threshold size over a given time interval (Beers 1962). Scientists have observed success in quantifying the stochastic nature of ingrowth through the use of mixture models that determine ingrowth occurrence and abundance (Fortin and DeBlois 2007; Li et al. 2011).

A challenge to modeling recruitment across diverse forests is incorporating the widespread herbivory pressure on palatable tree species (Larouche et al. 2010; Palik et al. 2015; Tanentzap et al. 2009). Since the 1950s, white-tailed deer (*Odocoileus virginianus* Zimmerman) have influenced forest vegetation dynamics in the northern United States (US) by reducing tree and shrub species diversity (Frerker et al. 2014). Herbivory has long been recognized as a detriment to forest regeneration of specific species across the northern US, including northern white-cedar (*Thuja occidentalis* L.) (Boulfroy et al. 2012; Larouche et al. 2010; Palik et al. 2015), oaks (*Quercus* spp.) (Wakeland and Swihart 2009), and eastern white pine (*Pinus strobus* L.) (White 2012). Hence, browse impacts are important covariates to consider when modeling tree recruitment. Similarly, deer may impact forests indirectly by altering availability of suitable habitat for other wildlife and forest-dependent species (Rooney and Waller 2003). Fortunately, methodologies for assessing browse impacts have recently been incorporated into a variety of forest inventories (McWilliams et al. 2015; Pierson and DeCalesta 2015; Sullivan et al. 2016).

Browse frequency is related to the availability of palatable species within a given forest area (Bradshaw and Waller 2016; Mudrak et al. 2009; White 2012). While experimental studies that employ

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Table 1. Mean (minimum and maximum in parentheses) of ingrowth characteristics on forest inventory plots (n = 2029) across the northern United States.

Size class[a]	Mean ingrowth (trees·ha^{-1}·5 years^{-1})	Mean proportion of basal area in palatable species	Plots with ingrowth	
			No.	%
Saplings	104 (0, 2849)	0.16 (0, 1)	879	43%
Overstory trees	16 (0, 241)	0.35 (0, 1)	1508	74%

[a]Size class threshold diameters are 2.5 cm for saplings and 12.7 cm for overstory trees.

fenced exclosures to eliminate herbivory pressure are useful to assess the recruitment potential of forests, the degree to which a range of browse impacts (e.g., low, medium, and high) influences recruitment is largely unknown. Recruitment can be quantified separately into sapling (trees 2.5–12.7 cm diameter at breast height (DBH)) and overstory tree (≥12.7 cm DBH) size classes given the strong role of understory and overstory tree density and composition in regulating tree recruitment (Bataineh et al. 2013; Bradshaw and Waller 2016).

The objective of this study is to model recruitment dynamics of saplings and overstory trees across diverse forests in the northern US. Specific objectives are to (1) quantify sapling and overstory tree recruitment patterns along a categorical gradient of browse impact, (2) compare models that estimate sapling and overstory tree recruitment as a function of stand characteristics within four browse impact classes, and (3) determine the proportion of ingrowth in palatable tree species subject to herbivory.

Methods

Study area

Forests across the northern US are comprised of conifer- and hardwood-dominated types. The study area ranged eastward from the state of Minnesota to Maine in the north and from Missouri to Maryland in the south. For conifers, 76% of growing stock volume is contained by species groups including pine (*Pinus* spp.), spruce (*Picea* spp.), balsam fir (*Abies balsamea* (L.) Mill.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). For hardwoods, no single species group dominates growing stock volume, but maples (*Acer* spp.) and oaks are most abundant (Oswalt et al. 2014).

Forest Inventory and Analysis data

Forest inventory data (n = 2029 plots) were acquired from the US Forest Service's Forest Inventory and Analysis (FIA) database (https://apps.fs.usda.gov/fiadb-downloads/CSV/datamart_csv.html; download date 28 December 2016; Table 1; Fig. 1). Plots were collected at a scale of approximately 1 plot per 19 400 ha. Specifically, we used the following data tables from the FIA database in this analysis: PLOT (e.g., inventory plot location), COND (e.g., plot condition and status such as forest type), TREE (e.g., number of existing and ingrowth trees), SEEDLING (e.g., number of tree seedlings), and PLOT_REGEN (e.g., deer browse impact on a plot). Only forested plots with all subplots observed under a single forest condition were used in the analysis. Inventory plots consisted of four 7.32 m fixed radius subplots for a total plot area of approximately 0.07 ha. All overstory live and standing dead trees with a DBH of at least 12.7 cm were measured on these subplots. Within each subplot, a 2.07 m microplot was established in which saplings with a DBH between 2.5 and 12.7 cm were measured. Ingrowth was observed from only the most recent remeasurement on each FIA plot (occurring between 2012 and 2015, with an initial measurement occurring between 2007 and 2010), thus avoiding the inclusion of repeated samples from the same plot over time.

The time interval between two measurements ranged from 5 to 15 years, with most having a 5-year remeasurement interval (89% of observations). Ingrowth trees, separated by saplings (threshold DBH = 2.5 cm) and overstory trees (threshold DBH = 12.7 cm), were defined as new tally trees on remeasured plots that did not qualify as through growth. The number of ingrowth trees observed in an FIA plot was standardized to a 5-year measurement length, rounded to the nearest integer, and expressed on a per-hectare basis for saplings and overstory trees.

Using data from the FIA's PLOT_REGEN table, browse impact was defined as the amount of pressure that herbivores exert on tree seedlings and other understory flora for the area surrounding the sample plot (McWilliams et al. 2015). This includes the consumption of shoots, twigs, and leaves of trees and shrubs used by animals for food (USDA Forest Service 2014). Four browse impact codes were used in this analysis: none (no browsing observed; vigorous seedlings present), medium (browsing evidence observed but not common; seedlings common), high (browsing evidence common), and very high (browsing evidence omnipresent or severe browse line evident). Plots that were located within a well-maintained exclosure were not used in this analysis.

To investigate objective 3, we identified palatable species within our database. The proportion of basal area in palatable tree species was determined for each FIA plot and related to ingrowth for saplings and overstory trees. The following palatable species as indicated by Rawinski (2014) as preferred and staple tree species were identified: red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), flowering dogwood (*Cornus florida* L.), Atlantic white-cedar (*Chamaecyparis thyoides* (L.) B.S.P), white ash (*Fraxinus americana* L.), eastern redcedar (*Juniperus virginiana* L.), cucumbertree (*Magnolia acuminata* L.), sweet bay (*Magnolia virginiana* L.), black gum (*Nyssa sylvatica* Marsh.), aspen (*Populus* spp.), cherries (*Prunus* spp.), oaks, northern white-cedar, American basswood (*Tilia americana* L.), and eastern hemlock.

Estimating ingrowth occurrence and abundance

Count regression models are useful for estimating ingrowth on remeasured forest inventory plots (Fortin and DeBlois 2007; Li et al. 2011). The Poisson (P) and negative binomial (NB) distributions were employed to test their effectiveness in accounting for the variability of ingrowth presence and abundance across the region. Negative binomial models are count models that include an overdispersion parameter, making them more flexible than Poisson models when estimating ingrowth abundance (Li et al. 2011). To account for data with a high proportion of zeros, e.g., whether or not ingrowth occurred on FIA plots, zero-inflated P (ZIP) and NB (ZINB) models were also examined. Both ZIP and ZINB models are types of mixture models that estimate structural and stochastic zeroes (Welsh et al. 1996).

A P probability is estimated by the mass function

$$(1) \qquad f_P(y) = \frac{\lambda^y e^{-\lambda}}{y!}$$

where y denotes the ingrowth count (trees·ha^{-1}·5 years^{-1}) and λ is the ingrowth mean. In the ZIP model, zero counts are estimated from a binomial or Poisson distribution. A ZIP probability is estimated by the mass function

$$(2) \qquad f_{ZIP}(y) = \begin{cases} \pi + (1 - \pi)e^{-\lambda} & y = 0 \\ (1 - \pi)f_P(y) & y = 1, 2, 3, \ldots \end{cases}$$

where π is the probability of zero occurrence, λ is estimated using independent predictor variables, and $f_P(y)$ is the right-hand side of eq. 1. In the case of the Poisson distribution, the variance is equal to its mean.

Fig. 1. Observed frequency of ingrowth for saplings and overstory trees by browse impact class on forest inventory plots (n = 2029) across the northern United States.

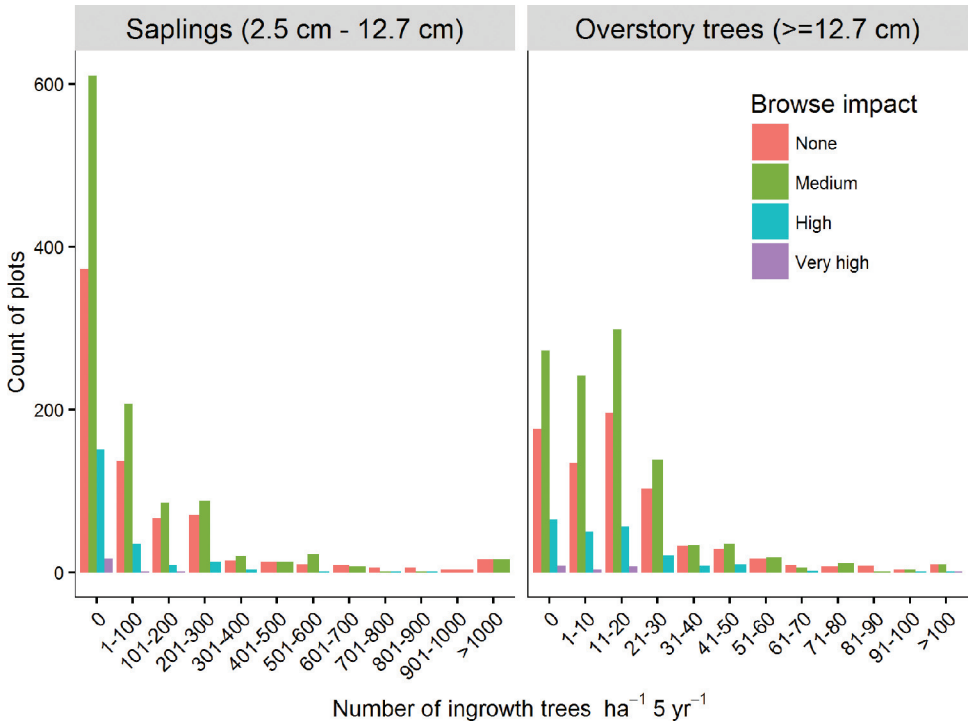


Table 2. Fit statistics of models fitted to ingrowth data for all species using Poisson, zero-inflated Poisson (ZIP), negative binomial (NB), and zero-inflated negative binomial (ZINB) approaches.

	AIC		Pearson's χ^2/df	
Model	Saplings (2.5–12.7 cm)	Overstory trees (≥12.7 cm)	Saplings (2.5–12.7 cm)	Overstory trees (≥12.7 cm)
Poisson	393 280	42 562	2.09	2.90
ZIP	162 790	28 792	1.12	2.47
NB	28 371	16 223	0.04	0.58
ZINB	13 621	14 036	0.96	1.91

The NB model differs from the P distribution by incorporating an overdispersion parameter α. Overdispersion reflects that the actual variances of observations exceed the nominal variances of identified distributions (Poortema 1999). An NB probability, obtained as a gamma mixture of P distributions, is estimated by the mass function

$$(3) \quad f_{NB}(y) = \frac{\Gamma(y + 1/\alpha)}{\Gamma(y + 1)\Gamma(1/\alpha)}\left(\frac{1}{1 + \lambda\alpha}\right)^{1/\alpha}\left(\frac{\lambda\alpha}{1 + \lambda\alpha}\right)^{y}$$

where y denotes the ingrowth count and λ is the ingrowth mean. The ZINB probability is estimated by the mass function

$$(4) \quad f_{ZINB}(y) = \begin{cases} \pi + (1 - \pi)\left(\frac{1}{1 + \lambda\alpha}\right)^{1/\alpha} & y = 0 \\ (1 - \pi)f_{NB}(y) & y = 1, 2, 3, \ldots \end{cases}$$

where $f_{NB}(y)$ is the right-hand side of eq. 3 and all other variables are as previously defined. For the λ parameter in the models, each was related to a system of linear predictors using a vector of explanatory variables and regression coefficients to be estimated.

Initial stand basal area (BA; m^2·ha^{-1}) for trees > 2.5 cm and browse impact classes were used as predictors of ingrowth occurrence and abundance. Results from similar regions have indicated that greater stand density decreases ingrowth abundance (Ek 1974; Fortin and DeBlois 2007; Li et al. 2011). Given the widely studied relationships between herbivory and tree abundance (e.g., Côté et al. 2004; Frelich and Lorimer 1985; Frerker et al. 2014; Nuttle et al. 2014), greater browse impact measured on FIA plots was hypothesized to decrease ingrowth and would seemingly be an important variable to consider when characterizing ingrowth occurrence and abundance across a large geographic region such as the northern US. Browse impact was specified as an indicator variable for each FIA plot. Similarly, the number of seedlings·ha^{-1} (SEED; from the FIA seedling table) and the maximum sapling DBH (MaxDBH$_{SAP}$; cm) observed on an FIA plot were used as predictor variables for ingrowth into the sapling and overstory tree classes, respectively. For determining overstory tree ingrowth, we also examined the mean and minimum sapling DBH on an FIA plot during initial analyses. Although significant to the models, those variables yielded a greater Akaike information criterion (AIC) value (Akaike 1974) than when MaxDBH$_{SAP}$ was specified. We hypothesized that greater quantities for SEED and MaxDBH$_{SAP}$ would indicate a higher probability of tree recruitment.

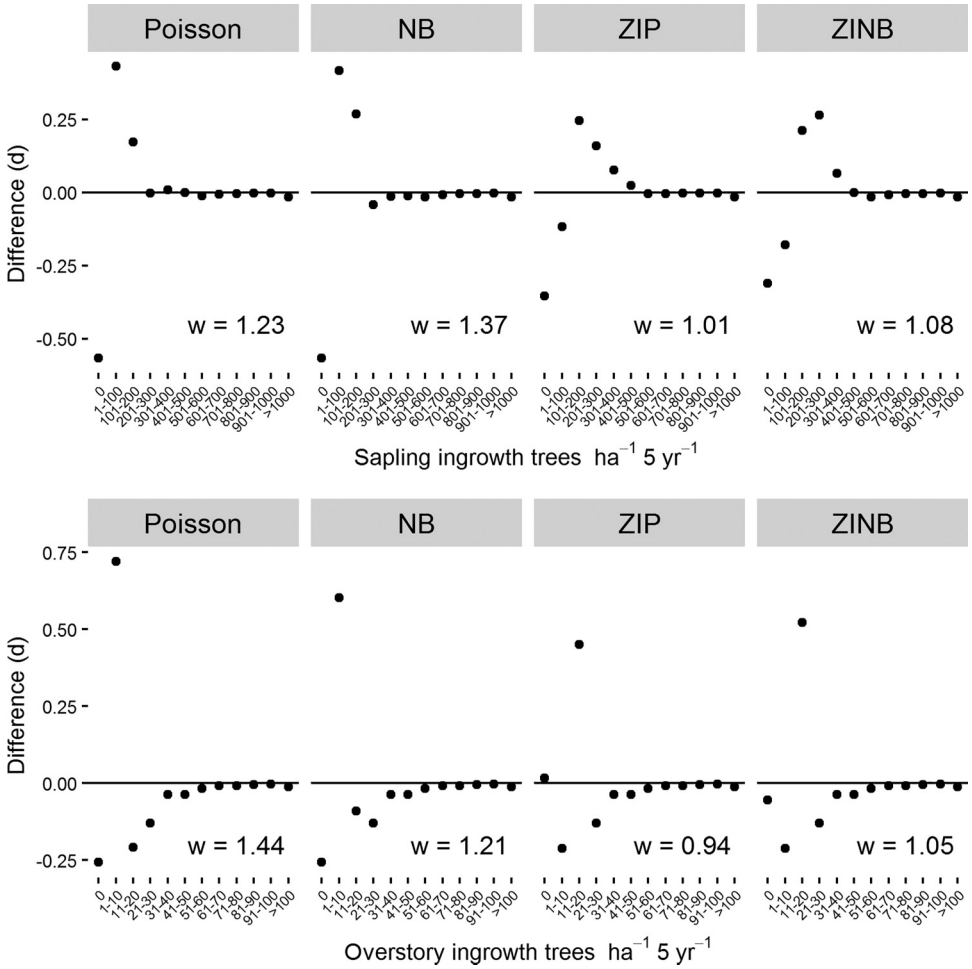
Log odds and log-link functions were used to model variation in the means of ingrowth absence and positive counts (abundance), respectively, for both saplings and overstory trees. For saplings, the log-link function for the models describes λ_{SAP} as

$$(5) \quad \ln(\lambda_{SAP}) = \beta_0 + \beta_1 BA + \beta_2 \log(SEED + 0.01) + \beta_3 BI_{MED} + \beta_4 BI_{HIGH} + \beta_5 BI_{VHIGH}$$

where β_i represents parameters to be estimated for the P or ZIP approach, and BI$_{MED}$, BI$_{HIGH}$, and BI$_{VHIGH}$ are indicator variables for plots measured under medium, high, and very high browse impact, respectively.

For overstory trees, the parameter estimates for the three browse impact indicator variables were consistently nonsignificant and included zero in the estimated 95% confidence interval.

Fig. 2. Diagnostic plots for the Poisson, zero-inflated Poisson (ZIP), negative binomial (NB), and zero-inflated negative binomial (ZINB) models displaying the difference (*d*) between the predicted probability and the observed proportion,where *w* is the sum of absolute values of *d*.



Instead we used a sole indicator variable to designate browse impact for overstory trees, where $BI_{HIGH–VHIGH}$ designates 1 for a plot with a high or very high browse impact and 0 otherwise. The log-link function for the P and ZIP and NB and ZINB models for overstory trees was

$$\ln(\lambda_{OVER}) = \beta_0 + \beta_1 BA + \beta_2 MaxDBH_{SAP} + \beta_3 BI_{HIGH-VHIGH} \quad (6)$$

The logistic equations characterizing the π parameter for ZIP and ZINB models were

$$\pi_{SAP} = \frac{1}{1 + \exp\{-[\gamma_0 + \gamma_1 BA + \gamma_2 \log(SEED + 0.01) + \gamma_3 BI_{MED} + \gamma_4 BI_{HIGH} + \gamma_5 BI_{VHIGH}]\}} \quad (7)$$

$$\pi_{OVER} = \frac{1}{1 + \exp[-(\gamma_0 + \gamma_1 BA + \gamma_2 MaxDBH_{SAP} + \gamma_3 BI_{HIGH-VHIGH})]} \quad (8)$$

for the sapling and overstory tree models, respectively, and γ_i represents parameters to be estimated. Relative model fits of the P, NB, ZIP, and ZINB approaches were evaluated using AIC to compare model performance. Initial modeling efforts that incorporated plots as random effects led to problems with convergence and (or) biologically unreasonable parameter estimates. Parameters for eqs. 5–8 were estimated using the NLMIXED procedure available in the SAS/STAT® software system (SAS Institute Inc. 2011).

Diagnostic plots that depict differences between predicted and observed probabilities, denoted *d*, were used to examine model fit (Lambert 1992). These plots allow one to examine unaccounted-for trends in models, which indicate overestimations or underestimations across adjacent predictions of ingrowth size classes (Fortin and DeBlois 2007). The values of *d* are computed as

$$d = \sum_{i=1}^{n} \left[\frac{\text{Prob}(y_i = k)}{n}\right] - \frac{\#(y_i = k)}{n} \quad (9)$$

where *n* is the number of observations, # is the frequency within the data, and *k* is the count. For an individual model, the sum of the absolute values of *d* was calculated and denoted *w*.

Pearson's chi-square (χ^2) statistics were also calculated to determine goodness of fit and were defined as

$$\chi^2 = \sum_{i=1}^{n} \left\{ \frac{[y_i - E(y_i)]^2}{\mathrm{Var}(y_i)} \right\} \quad (10)$$

where y_i is the observed number of sapling or ingrowth trees. The expected value $E(y_i)$ and variance $\mathrm{Var}(y_i)$ were calculated for the response variable under the specified model probability assumption (e.g., P, NB, ZIP, or ZINB) according to Zuur et al. (2009). A good model fit is indicated if the ratio of the χ^2 to its degrees of freedom (χ^2/df) is close to one.

Estimating palatable tree ingrowth

Beta regression techniques were used to determine the proportion of ingrowth tree basal area for palatable species (ING_{PALBA}). The independent variables were initial stand basal area and the proportion of basal area in palatable species at previous measurement ($BA_{PALAT,\ t-1}$). Beta regression allows the estimation of continuous variables that assume values as rates or proportions (Ferrari and Cribari-Neto 2004). Given that the proportion of ingrowth tree basal area for palatable species included both 0 and 1 for the FIA plots, we transformed the response variable by $(ING_{PALBA} \times [n-1] + 0.5)/n$, where $n = 2029$ is the total number of FIA plots (Smithson and Verkuilen 2006). The equation is given as

$$ING_{PALBA} = \frac{\exp(\nu_0 + \nu_1 BA + \nu_2 BA_{PALAT,\ t-1})}{1 + \exp(\nu_0 + \nu_1 BA + \nu_2 BA_{PALAT,\ t-1})} \quad (11)$$

where ν_i represents parameters to be estimated separately for saplings and overstory trees. Parameters for eq. 11 were estimated using the GLIMMIX procedure available in the SAS/STAT® software system (SAS Institute Inc. 2011).

Results

For the 2029 plots analyzed, zero ingrowth was observed on 57% and 26% of all plots in the sapling (≥2.5 cm DBH) and overstory tree (≥12.7 cm DBH) size classes, respectively. Average ingrowth was 104.2 ± 233.5 (mean ± SD) and 16.1 ± 21.4 trees·ha^{-1}·5 years^{-1} for saplings and overstory tree size classes, respectively (Table 1). In plots with high or very high browse impact (n = 233 plots), zero ingrowth was observed on 72% of plots in the sapling size class and on 31% of plots in the overstory tree size class (Fig. 1). Total basal area across all plots averaged 23.2 m^2·ha^{-1} (range from 0.1 to 62.5 m^2·ha^{-1}), and stem density averaged 664.5 trees·ha^{-1} (range from 6.0 to 8807.0 trees·ha^{-1}). Average number of seedlings per hectare was 6614 ± 7696, and mean $MaxDBH_{SAP}$ was 8.0 ± 3.8 cm.

Given the high observed variance to mean ratios for sapling (523.2) and overstory tree ingrowth (28.4), overdispersion was shown in the response variable. Both the NB and ZINB models had significantly lower AIC values when compared with the P and ZIP models, providing justification for incorporating the overdispersion parameter by using NB and ZINB models. The ZINB model resulted in the lowest values for AIC when comparing the four model forms. The Pearson χ^2 statistic indicated that ZIP and ZINB models were favorable for describing sapling ingrowth patterns and that NB and ZINB models provided a better fit for overstory trees, as indicated in Table 2.

The standard P and NB models were not able to estimate ingrowth on plots in which zero observations occurred. The P and NB models overestimated abundance in smaller ingrowth classes (e.g., 1 to 100 and 1 to 10 trees·ha^{-1}·5 years^{-1} for saplings and overstory trees, respectively). For saplings, the ZIP and ZINB models tended to overestimate abundance in smaller ingrowth classes, while for overstory trees, these models tended to underestimate abundance in smaller ingrowth classes. Values for w indicated that the differences (d) tended to be closer to zero for the ZIP and ZINB models (Fig. 2).

Table 3. Estimated parameters for the zero-inflated negative binomial model for determining ingrowth of saplings and overstory trees for all species in the northern United States.[a]

Parameter	Estimate	SE	p value
Saplings (2.5–12.7 cm)			
γ_0 (intercept)	3.8350	0.3859	<0.0001
γ_1 (BA)	0.02884	0.004726	<0.0001
γ_2 (SEED + 0.01)	−0.5341	0.04410	<0.0001
γ_3 (BI_{MED})	0.1277	0.1036	0.2179
γ_4 (BI_{HIGH})	0.2974	0.1845	0.1072
γ_5 (BI_{VHIGH})	3.8103	1.9384	0.0495
β_0 (intercept)	4.6804	0.1384	<0.0001
β_1 (BA)	−0.02140	0.002351	<0.0001
β_2 (SEED + 0.01)	0.1528	0.01332	<0.0001
β_3 (BI_{MED})	−0.1780	0.05629	0.0016
β_4 (BI_{HIGH})	−0.4811	0.1094	<0.0001
β_5 (BI_{VHIGH})	−0.6939	0.6216	0.2644
Overstory trees (≥12.7 cm)			
γ_0 (intercept)	−0.5990	0.1553	<0.0001
γ_1 (BA)	0.01491	0.005091	0.0034
γ_2 ($MaxDBH_{SAP}$)	−0.1154	0.01357	<0.0001
γ_3 ($BI_{HIGH–VHIGH}$)	0.2019	0.1622	0.2135
β_0 (intercept)	2.4896	0.06053	<0.0001
β_1 (BA)	−0.00883	0.001932	<0.0001
β_2 ($MaxDBH_{SAP}$)	0.08477	0.005259	<0.0001
β_3 ($BI_{HIGH–VHIGH}$)	−0.1453	0.06437	0.0241

Note: BA, initial stand basal area; SEED, number of seedlings·ha^{-1}; $MaxDBH_{SAP}$, maximum sapling diameter at breast height; BI_{MED}, BI_{HIGH}, BI_{VHIGH}, and $BI_{HIGH–VHIGH}$, indicator variables for plots measured under medium, high, very high, and high + very high browse impacts, respectively.

[a]Estimated parameters for eqs. 5–8.

Initial stand basal area and increased severity of browse impact had negative effects on ingrowth abundance (Table 3; Fig. 3). For the average stand basal area (23.2 m^2·ha^{-1}), models indicated that sapling ingrowth in stands with very high browse impact would contain 50.0% fewer ingrowth individuals compared with stands with no browse impact. Lower browse impact was predicted for overstory trees, where models indicated that ingrowth in stands with a high or very high browse impact would contain 16.7% fewer ingrowth trees compared with stands with no or medium browse impact. A higher number of seedlings per hectare and a greater $MaxSAP_{DBH}$ indicated greater predicted recruitment into the sapling and overstory tree classes, respectively. We also examined the mean DBH of saplings and total number of saplings per hectare as covariates in these models but observed a lower AIC when $MaxSAP_{DBH}$ was used in lieu of these variables. The ZINB models similarly indicated a decreased probability of ingrowth occurrence in the sapling and overstory tree classes as browse impact and stand density increased.

When determining ingrowth of palatable species, models indicated a decreasing proportion of ingrowth basal area in palatable tree species as stand density decreased. All parameters were significant at the $\alpha < 0.05$ level with the exception of the coefficient associated with initial stand basal area for the overstory tree model (Table 4). For the same stand conditions, models indicated that the proportion of ingrowth basal area in palatable species would be less for saplings than for overstory trees (Fig. 4).

Discussion

Models from this analysis suggest that forests with very high browse impacts will result in a 50% reduction of sapling recruitment compared with those with no observed browse impacts. Although differences in recruitment into overstory tree size classes were less apparent between no to medium browse impacts

Fig. 3. Expected recruitment given ingrowth occurrence for (*a*, *b*) saplings and (*c*, *d*) overstory trees by browse impact class and basal area (BA) across the northern United States, based on the fitted zero-inflated negative binomial model.

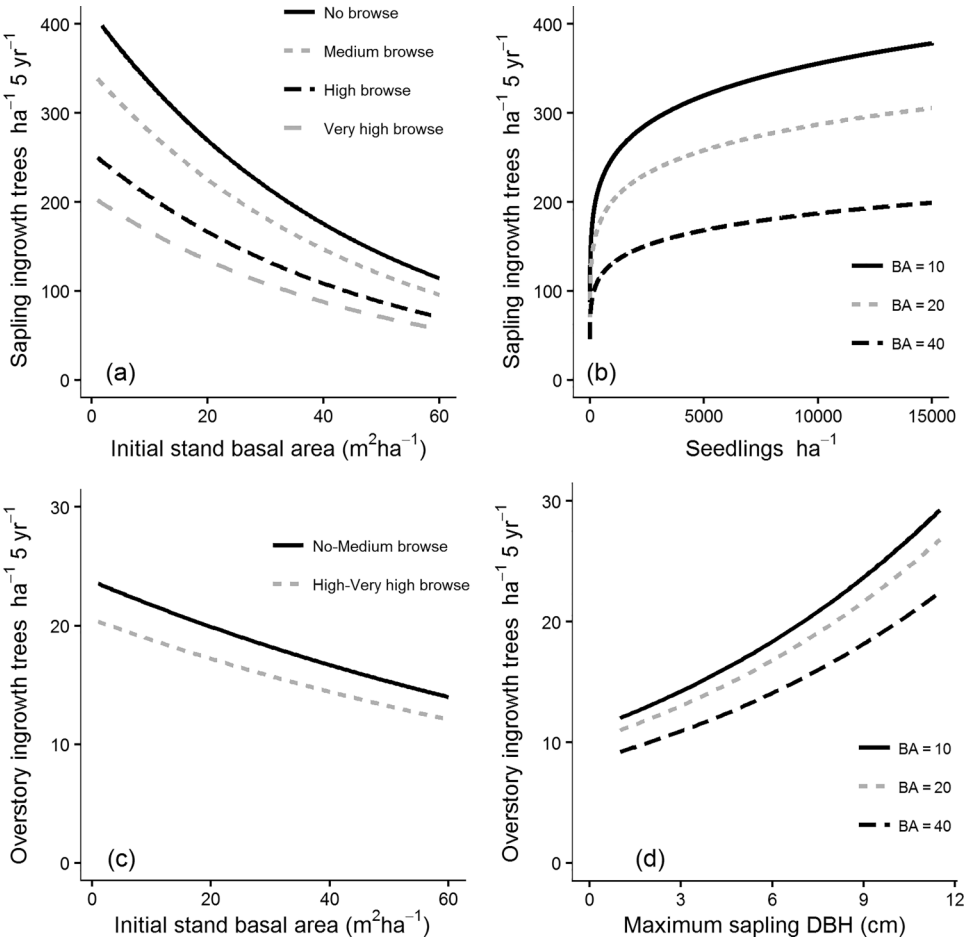


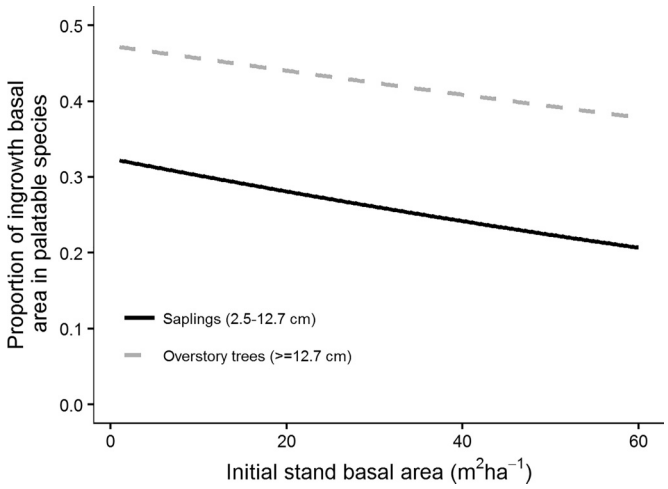
Table 4. Estimated parameters for the beta regression model determining the proportion of ingrowth basal area for saplings and overstory trees for all species in the northern United States.[a]

Parameter	Estimate	SE	*p* value
Saplings (2.5–12.7 cm)			
ν_0 (intercept)	−0.9151	0.08347	<0.0001
ν_1 (BA)	−0.00980	0.00270	0.0003
ν_2 ($BA_{PALAT,t-1}$)	0.2653	0.09189	0.0039
Overstory trees (≥12.7 cm)			
ν_0 (intercept)	−0.8611	0.08605	<0.0001
ν_1 (BA)	−0.00521	0.00283	0.0654
ν_2 ($BA_{PALAT,t-1}$)	0.9915	0.09687	<0.0001

Note: BA, initial stand basal area; $BA_{PALAT,t-1}$, proportion of basal area in palatable species at previous measurement.

[a]Estimated parameters for eq. 11.

Fig. 4. Predicted proportion of ingrowth tree basal area in palatable species for saplings and overstory trees in the northern United States, assuming a basal area proportion in palatable species of 0.50.



and high to very high browse impacts, herbivory impacts clearly play a role in determining forest composition and density for the variety of forest types across the northern US. Deer densities vary considerably across the northern US region (Walters et al. 2016). For example, densities have been as high as 23 deer·km^{-2} in northern Wisconsin (Bradshaw and Waller 2016) and 29.9 deer·km^{-2} in western New York (Rudolph et al. 2000) in recent decades. Less than 40% of the area of northern US forests may have deer densities of less than 4 deer·km^{-2} (Russell et al. 2017), which has been suggested as a threshold at which deer densities could provide detrimental impacts to browse-sensitive tree seedlings (Alverson et al. 1988). Because of this, managers should rely on useful tools to assess the impacts of herbivory in forest regeneration planning. Although a full cycle of the FIA regeneration protocol and browse impacts have yet to be collected, initial analyses highlight important spatial trends across the northern US (McWilliams and Westfall 2015). These findings provide tools for a thorough assessment of

the role that silvicultural techniques play in promoting or deterring herbivory (e.g., retaining coarse woody materials to obstruct browse) in addition to understanding the presence and abundance of browse-sensitive species.

Although this study emphasized total recruitment into the sapling and overstory tree size classes, species-specific models of recruitment in the future can likely focus on localized regions with attributes specific to each species as predictors (e.g., density of the target species and palatability ranking). In mixed-species stands in the Acadian region of North America, Li et al. (2011) grouped over 50 species into seven genera to determine the percentage of ingrowth tree basal area by species group. If browse palatability is known for the species occupying a general area (e.g., Bradshaw and Waller 2016; Wakeland and Swihart 2009), recruitment could similarly be modeled by species palatability class within a system of equations. Such a ranking of species palatability would aid researchers in modeling efforts that emphasize select species in targeted geographic areas.

If forest management actions are undertaken to eliminate herbivory impacts, including exclosures (Frerker et al. 2014; Palik et al. 2015; White 2012) and enclosures (Horsley et al. 2003; Nuttle et al. 2014), palatable species can survive and grow at levels similar to those of nonpalatable species. Adequately capturing self-thinning dynamics through stand conditions such as relative density (e.g., Ducey et al. 2017) could link browse impacts with forest dynamics. Nonpalatable species may similarly have competitive height growth advantages over palatable species (Palik et al. 2015), requiring the need for monitoring individual tree measurements in studies that seek to understand forest management impacts on recruitment.

The finding that less than half (43%) of FIA plots contained ingrowth observations into the sapling size class is somewhat similar to what Li et al. (2011) observed (30.1%) using data sources with multiple minimum threshold diameters over a similar measurement interval. The stochastic nature of ingrowth observations necessitates the use of zero-inflated modeling strategies in modeling tree recruitment (Fortin and DeBlois 2007; Li et al. 2011). The superior performance of the ZINB model relative to other model forms captures the overdispersion present in ingrowth observations, as seen in the high observed variance to mean ratios. Random effects that capture plot-to-plot variability may similarly be employed to capture regional- and plot-level variability. However, Li et al. (2011) found that plot-level random effects were not correlated with site factors such as elevation and soil drainage.

As shown in other studies (Ek 1974; Fortin and DeBlois 2007; Li et al. 2011), increasing stand basal area decreased the abundance of ingrowth observations, a reflection of stand development stage. Ingrowth may be more abundant on higher quality sites (Hann 1980; Li et al. 2011); however, the expansive study region examined here largely precluded the investigation of site quality metrics as a potential covariate of ingrowth due to the numerous tree species and site conditions across the northern US. Climate-derived estimates of site productivity using nonparametric approaches may prove useful in the future when modeling ingrowth across broad geographic regions (e.g., Li et al. 2011; Weiskittel et al. 2011*b*). To our knowledge, predictor variables that depict attributes from smaller size classes (e.g., the number of seedlings per hectare in the case of saplings and $MaxDBH_{SAP}$ in the case of overstory trees) have not been used in the models of forest tree recruitment. Additional variables such as species-specific basal area, forest type, stand size class, and whether or not a disturbance or treatment occurred could similarly be examined as predictors of ingrowth. Such attributes are often readily available from forest inventory records, and these results show their usefulness in predicting the probability and abundance of ingrowth.

With additional remeasurements and analyses, selection of the appropriate time interval may be required to accurately determine recruitment levels. The probability and abundance of ingrowth increases with a longer time step; however, modelers of tree recruitment typically standardize ingrowth to a common interval such as annually (e.g., Li et al. 2011) or 10 years (e.g., Shifley et al. 1993). Additional remeasurements may allow users to specify an interval of interest in simulating recruitment patterns under a variety of stand conditions and browse impacts. The size of plots also determines the probability and abundance of ingrowth, as large plots display higher rates of ingrowth compared with smaller plots (Li et al. 2011). In addition to recruitment models that focus on DBH measurements, modeling growth of trees above specified height thresholds (e.g., 2 m; Bradshaw and Waller 2016) can quantify the rate at which trees grow above browse height and free from herbivory.

Additional ecological problems with herbivory and, in particular, high white-tailed deer densities include a greater presence and abundance of invasive plants (Knight et al. 2009; Russell et al. 2017) and seed dispersal of non-native species (Myers et al. 2004; Williams and Ward 2006). Coupled with trends in mean annual temperature and overstory tree diversity (e.g., Bose et al. 2016), deer browse impacts can be potential covariates in metrics of forest biodiversity such as species richness in the sapling size class. As observed in this study, different browse impact indicator variables were suited to different size classes; these findings indicated the differences in herbivory impacts to saplings and overstory tree size classes. Species richness and density can be summarized using information from national forest inventories, providing further insights into not only abundance but also the composition and structure of species that shape tree recruitment. Given that higher browse impacts decrease recruitment, they play a tremendous role in altering tree composition and shaping long-term forest vegetation dynamics (Frerker et al. 2014). In forests with herbivory pressure, browse impacts should be incorporated into models that quantify the presence and abundance of tree recruitment.

Conclusions

These findings suggest the need for incorporating browse impact assessments in models of tree recruitment in regions where herbivory impedes successful forest regeneration. Using emerging data that monitors browse impacts across diverse forests in the northern US, this study observed that recruitment in forests with high browse impacts reduced sapling and overstory tree ingrowth by 50.0% and 16.7%, respectively. It can be hypothesized that such substantial levels of browse are altering trajectories of stand development and species composition, confounding silvicultural objectives. Despite the stochastic nature of ingrowth observations, this study observed that modeling ingrowth using mixture models provided a useful framework for accounting for browse impacts, which can subsequently be implemented in forest growth and yield models.

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