



# Deer browsing and shrub competition set sapling recruitment height and interact with light to shape recruitment niches for temperate forest tree species



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## ABSTRACT

For temperate forests, Michigan, USA, we asked: (1) does evidence exist for a height-dependent sapling recruitment bottleneck caused by shrub layer competition and white-tailed deer (*Odocoileus virginianus*) browsing and, if so, (2) how do these factors interact with light availability in shaping species-specific sapling recruitment niches? The combination of deer browsing effects on tree population height structure and the effects of deer and shrubs on tree seedling height and mortality indicate a shrub-deer bottleneck for sapling recruitment. The maximum height of deer browsing and shrub canopies as well as height dependent seedling mortality rates revealed a critical height threshold of approximately 2 m, above which trees escape from shrub and deer effects (i.e. sapling recruitment). Species' sapling recruitment niches differed across a harvest gap size (i.e. light availability) gradient, over which tree seedling height growth potential and shrub competition increased with gap size, but deer browsing probability decreased. Specific to forests with high deer populations, niche differences were related to species growth and survival properties, with species generally falling into three groups: *High Light*, *Broad*, and *Nowhere*. *High Light* species incur high mortality from shade, shrub competition, and deer browsing. However, recruitment can occur in recently formed large gaps, where seedlings growing within developing shrub canopies avoid competition via rapid height growth and are partially protected from browsing deer. *Broad* species have lower mortality in shade and grow slower than *High Light* species and, compared to other groups, exhibit height growth and mortality rates that are less-sensitive to deer browsing pressure. These properties allows sapling recruitment of *Broad* species over a wide range of gap sizes, including larger gaps, where, via advance regeneration, they can avoid competition with developing shrub layers following canopy disturbance. *Nowhere* species are similar to *Broad* species, except their height growth and mortality are sensitive to deer browsing pressure. Heavy browsing pressure in smaller gaps and an inability to maintain taller advance regeneration to contend with shrub competition when large gaps form leave *Nowhere* species without a sapling recruitment niche. In conclusion, we provide evidence that shrub competition, ungulate browsing, harvest gap size and their interactions constrain height-specific sapling recruitment among tree species in the temperate forests of Michigan. Similar mechanisms may operate in other forests with high ungulate populations. Given these drivers and current management regimes, increasing tree species diversity and resilience to future disturbances may hinge on changing and integrating forest and ungulate management paradigms.

## 1. Introduction

In the temperate forest of Eastern North America and similar forests worldwide, shrub layer competition and ungulate browsing pressure may have a large influence on tree species regeneration niches (Dovciak et al., 2003, Côte et al., 2004, Royo and Carson, 2006, Kunstler et al., 2009, Kern et al., 2012, Nuttle et al., 2013, Walters et al., 2016,

Ramirez et al., 2018). These factors may act by asserting strong, species-specific effects on seedling to sapling size class transitions, with individuals transcending their height-dependent effects (hereafter called sapling recruits) strongly improving their odds of becoming mature trees.

The shrub layer can negatively affect sapling recruitment via light competition (Berkowitz et al., 1995, Royo and Carson, 2006), soil

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resource competition (Beckage and Clark, 2003, Montgomery et al., 2010, Randall and Walters, 2019), and mechanical damage (Hajek et al., 2015). If competition is primarily for light, the shrub layer would be expected to cause negative height-dependent mortality on trees subordinate to shrub canopies. Competitive effects should be strongest on small seedlings near the forest floor, where shrub canopies can reduce light by > 98% (George and Bazzaz, 1999, Walters et al., 2016), decrease with seedling height as light availability increases, and dissipate as saplings over-top shrubs (Royo and Carson, 2006). In turn, tree species may vary in their growth and survival responses to shrub competition via differences in height growth rate potential, shade tolerance and other properties (Beckage and Clark, 2003, Walters et al., 2016). Finally, the strength of light competition effects varies with shrub canopy density, which in turn varies with species composition, the timing and severity of forest overstory disturbance, soil resources, and other factors (Willis et al., 2016, Walters et al., 2016, Giesbrecht et al., 2017, Widen et al., 2018). Height-dependent competition from dense shrub layers could have large effects on the composition and density of sapling recruit populations.

Browsing of tree seedlings by white-tailed deer (*Odocoileus virginianus*, Zimmermann, hereafter referred to as deer) is severe over large extents of Eastern North America and can also limit sapling recruitment (Rooney and Waller, 2003, Côte et al., 2004, Matonis et al., 2011, McWilliams et al., 2018). Like shrubs, the effect of browsing deer should be strongly height-dependent and limited to their maximum browsing height. Similarly, deer browsing effects vary with many factors (e.g. spatial variation in deer density, Patton et al., 2018), and impacts of a given level of deer browsing pressure vary among tree species (Nuttle et al., 2013). Thus, the combination of abundant local deer populations and interspecific variation in sensitivity to deer browsing pressure could also strongly affect the composition and density of sapling recruit populations (Royo and Carson, 2006, Randall and Walters, 2011, Matonis et al., 2011, Nuttle et al., 2013, Bradshaw and Waller, 2016, Ward et al., 2017).

Quantifying the pattern and basis of shrub and deer effects on seedling to sapling recruit transitions could increase understanding and generalization of mechanisms underlying forest dynamics of temperate forests (Pacala et al., 1996, Lines et al., 2010, Kunstler et al., 2016, Needham et al., 2018). Regarding the basis, the probability of a seedling becoming a sapling recruit (i.e. growing taller than deer and shrub effects) depends on how quickly it is able to reach a threshold escape height and its probability of dying along the way (Pacala et al., 1996, Needham et al., 2018). Seedling height growth and survival sensitivities may often correlate positively; e.g. large declines in height growth lead to large declines in survival. However, differences in species carbohydrate allocation programs, morphology, shade tolerance, and other properties could lead to considerable orthogonal variation in height growth and survival sensitivities among species (Keyser, 2019). Furthermore, different species-level properties likely underlie growth and survival responses to shrub competition (e.g. shade tolerance) vs. deer browsing pressure (e.g. browsing preferences).

Patterns of sapling recruitment and their dependence on shrub competition and deer browsing pressure may vary over forested

landscapes with many factors. However, variation in canopy disturbance severity may be particularly important to consider. Understory light gradients resulting from variation in canopy disturbance severity is widely considered to be a dominant mechanism underlying tree species recruitment niches (Shugart, 1984, Runkle, 1985, Pacala et al., 1996), and is the primary target of forest harvest manipulations by forest managers (Webster et al., 2018). However, recent studies have shown that shrub competition and deer browsing can modify expected shade tolerance-based species partitioning of understory light gradients (Kern et al., 2013, Nuttle et al., 2013, Walters et al., 2016). Furthermore, light availability, shrub competition, and deer browsing may have complex interacting effects on interspecific sapling recruitment niches. For example, high shrub densities in large canopy harvest gaps have been shown to decrease the proportion of seedlings browsed by deer, potentially creating a recruitment niche for some species in the face of high deer populations (Harlow and Downing, 1969, Ripley and Campbell, 1960, Walters et al., 2016). However, the longer-term effects of these interacting factors on patterns of sapling recruitment among species and their basis in species properties are not well understood.

In summary, shrub competition and deer browsing may strongly limit sapling recruitment. If true, then the height structure of juvenile tree populations should reflect these bottlenecks, juvenile trees should exhibit negative height-dependent mortality to shrub competition and deer browsing, and critical height thresholds for sapling recruitment should be identifiable. Furthermore, shrub competition, deer browsing, and light availability may have interacting effects on sapling recruitment, with effects varying among species via differences in height growth and survival sensitivities to these factors, with implications for defining species-specific sapling recruitment niches. In this report, we address the following questions with data from temperate forests, Michigan, USA:

- (1) Is the height structure of juvenile tree populations consistent with a sapling recruitment bottleneck caused by deer browsing?
- (2) Can a critical height threshold for sapling recruitment (i.e. escape from shrub competition and deer browsing) be identified from maximum shrub canopy height, maximum deer browsing height, and patterns of height-dependent juvenile tree mortality?
- (3) How do shrub competition, deer browsing pressure, and light availability/harvest gap size interact to shape interspecific sapling recruitment niches?

## 2. Methods

We addressed our questions with data from natural and manipulative field experiments. Most data are from experiments with methodological details that are already published, but data in this report are either novel or are analyzed and presented differently in this paper. Table 1 includes relevant information regarding each data set (sometimes multiple data sets per study), and references to prior studies they are associated with.

**Table 1**  
Summary of data sources used for this report.

Study name	Objective	Sites	Dominant overstory species	Species planted	Light environment	Deer density km <sup>-1</sup>	Shrub competition
NH_NAT	Sapling height structure*	59	<i>Acer saccharum</i>	n/a	347 gaps (80–915 m <sup>2</sup> )	1–62	n/a
POP_NAT	Sapling height structure <sup>‡</sup>	60	<i>Populus</i> spp.	n/a	understory	11 vs. 17	n/a
PLANTED	Browsing height <sup>‡</sup>	1	<i>Acer saccharum</i>	16	44 gaps (0–3234 m <sup>2</sup> )	10.4	n/a
PLANTED	Shrub canopy height**	2	<i>Acer saccharum</i>	n/a	89 gaps (0–3234 m <sup>2</sup> )	n/a	yes
PLANTED	Sapling growth, mortality, recruitment**	1	<i>Acer saccharum</i>	16	44 gaps (0–3234 m <sup>2</sup> )	0 vs. 10.4	yes vs. no

\* Experimental design details in Matonis et al., 2011.

‡ Experimental design details in Randall and Walters 2011.

\*\* Experimental design details in Walters et al., 2014, 2016. n/a = does not apply to data objective.

## 2.1. Juvenile tree population height structure

Data on juvenile tree height structure was collected in two natural experiments: one study in northern hardwood stands (referred to as NH\_NAT) (Matonis et al., 2011, Table 1), and a second in *Populus* spp. stands (referred to as POP\_NAT) (Randall and Walters, 2011, Table 1). In NH\_NAT, 59 northern hardwood stands were located within a 4500-km<sup>2</sup> study area in the western Upper Peninsula of Michigan. The study area has a strong gradient of decreasing winter deer density and increasing winter snow-pack depth from south to north (Doepker et al., 1994; Shi et al., 2006). Sampled stands were dominated by *Acer saccharum* Marsh and managed by single-tree/small-group selection silviculture (Nyland, 1998). In each stand, vegetation sampling plots were located in 4–6 harvest gaps created 7–15 years before sampling. Gap sizes (Runkle, 1982) ranged from 80–915 m<sup>2</sup> with a median of 155 m<sup>2</sup> (Matonis et al., 2011). In each gap-centered plot, trees were tallied by species and height in either 1 m<sup>2</sup> quadrats (for seedlings 0–1 m tall) or in a 154 m<sup>2</sup> circular plot (for saplings 1–6 m tall). At each site, winter deer fecal pellet density, geo-coordinates, and snow depth were measured/estimated as proxies of deer browsing pressure (Matonis et al., 2011). Geo-coordinates are reported here as, among proxies, it was most consistently related to browsing-sensitive *A. saccharum* densities across size classes.

In the POP\_NAT study (Randall and Walters, 2011), data were collected on juvenile tree height structure in the understories of *Populus tremuloides* Michx./*Populus grandidentata* Michx. stands located on a 7317 ha private hunting club property (Mid Forest Lodge, MFL, 31 stands), and nearby (> 1.6 km and < 10 km from MFL property boundary) State of Michigan-owned lands (29 stands) in the central Lower Peninsula, MI, USA. *Populus* stands were closed canopy and had no history of partial harvests. Deer density estimates based on winter fecal pellet count data were 11.0 vs. 6.8 deer/km<sup>2</sup> on MFL vs. State land, respectively (Hill, 2000). Single-nested plot centers were established in each stand, and tree and shrub stem heights and density were tallied by species. Circular plot radii were 3.1 m for stems 0.24–1.4 m tall and 5.64 m for stems > 1.4 m tall and < 10 cm diameter at 1.4 m tall.

## 2.2. Maximum shrub canopy and deer browsing height; planted seedling growth and mortality responses to harvest gap light, shrubs, and deer

Data for assessing maximum canopy height of the *Rubus*-dominated shrub layer, maximum height of deer browsing, and tree seedling responses to light availability (i.e. harvest gap size), deer browsing pressure, and shrub density were all collected from PLANTED, a manipulative stand-scale experiment (Table 1, Walters et al., 2014, 2016). The study comprised two stands (31.7 ha and 18 ha), each with multiple harvest gaps of varying sizes located in mesic northern hardwood forests in the northern Lower Peninsula, Michigan, USA. In each stand, harvest gap-centered plots and unbroken overstory plots were established, with some subplots assigned to following natural vegetation dynamics and others planted with tree seedlings of multiple species. Planted seedling and deer browsing height data are from the 31.7 ha site, while shrub canopy height data are from both sites (Table 1). The deer density estimate for Emmet County (where the stands are located) was 10.4 deer km<sup>-2</sup> (Mattson and Moritz, 2008, Brent Rudolf, Wildlife Division, Michigan Department of Natural Resources). Given most data are from the 31.7 ha site and methods are mostly redundant, further description of the experiment are for the 31.7 ha stand.

At the 31.7 ha site, forty harvest gaps ranging in size from single-tree to 0.3 ha were harvested in the winter of 2009–2010. In spring 2010, we established plots at the center of the harvest gaps and in four unharvested areas. Plots were either fenced ( $n = 29$ ) to exclude deer or left unfenced ( $n = 15$ ). We planted one-year-old seedlings of 14 species into plots in spring 2011 (*Betula papyrifera* L., *Betula alleghaniensis* Britton., *Castanea dentata* (Marsh.) Borkh., *P. tremuloides*, *Ulmus*

*americana* L., *Juglans nigra* L., *Acer rubrum* L., *Quercus rubra* L., *Picea glauca* (Moench) Voss, *Pinus strobus* L., *Abies balsamea* (L.) Mill., *Tsuga canadensis* (L.) Carr., *Carya cordiformis* (Wangeh.) K. Koch, and *T. occidentalis* L.). Following tree planting, weeded (all non-tree vegetation clipped to ground height) and unweeded (vegetation allowed to grow) treatments were applied to seedling subplots. *Rubus* spp. shrubs dominated the shrub layer at our site. Therefore, in the PLANTED study, the fenced:unweeded treatment is referred to as *SHRUB*. Similarly, we refer to the unfenced:weeded treatment as *DEER*, unfenced:unweeded treatment as *DEER + SHRUB*, and fenced:weeded as *CONTROL*.

Planted seedlings surviving at the end of the first growing season were fitted with numbered tags, as were second-year seedlings of naturally established *Fraxinus americana* L. and *A. saccharum*. Seedling height and survival were determined annually in autumn, except for 2016 (determined early spring 2017). In some subplots where survival and growth were high, we removed some tagged trees to reduce competition by cutting aboveground portions. We removed seedlings without size bias relative to other seedlings of the same species in the same subplot/plot, which we confirmed with *post hoc* analyses of thinned vs. unthinned height (data not shown).

Harvest gap size was estimated by mapping tree boles and light availability was estimated as percent of open sky total transmission from analyses of hemispherical photographs (Frazer et al., 1999). The values depict light as modified only by the midstory and overstory trees at gap edge and beyond (i.e. vegetation above the shrub layer) and will hereafter be referred to as *GAP LIGHT*. Given its clear role in tree seedling growth and survival, we focus on *GAP LIGHT*, but discuss gap size when relevant (e.g. management implications).

The maximum height of the shrub canopy was determined for each unweeded planted subplot and unplanted subplots by ocular estimation with a calibrated height pole to the nearest cm using nine predetermined locations in a grid pattern within each subplot. Data on maximum browsing height was taken on seedlings that had been fenced to exclude deer for six years. A dense melting snowpack pulled fences down in March 2017, leading to the first deer browsing event for fenced seedlings since the inception of the project. For those previously-fenced saplings that sustained browsing damage, but were tall enough that at least the topmost axillary branches were not browsed, we determined the maximum height of browsed branch tips ( $n = 36$ , five different species).

## 2.3. Statistical analysis

### 2.3.1. Height structure of juvenile tree populations

Tree count data from the NH\_NAT and POP\_NAT studies were often overdispersed and zero-inflated, thus we focused on the most abundant species and used generalized regression models with negative binomial distributions to obtain maximum likelihood estimates and 95% confidence intervals (fit model platform, JMP). Due to imbalance across size classes, including lower  $n$  and a higher degree of zero inflation in larger size classes and for some species (e.g. *A. saccharum* in NH\_NAT study), we developed separate models by species and size class to estimate stem counts. Given the use of separate models by species and height class, we compare estimates by non-overlap of confidence intervals (i.e.,  $P < 0.01$ , Cumming and Finch, 2005). For the NH\_NAT data, we modeled stem counts by species and height class (1 m width classes from 0 to 6 m tall) as a function of northing, and generated estimates for the 10th percentile of northing (i.e. higher deer density) and the 90th percentile of northing (i.e. lower deer density) of our study area. We contrasted browsing-sensitive *A. saccharum* and browsing-insensitive *Ostrya virginiana* (Mill.) K. Koch (Burns and Honkala, 1990), which together comprised 75% of all stems taller than 1 m. For the POP\_NAT data, we modeled stem counts by height class (0.25–1.5 m, then 1 m width classes from 1.5 to 6.5 m tall) for the four most well-represented species or species groups (e.g., *Quercus velutina* Lamb. and *Q. rubra* were grouped as *Quercus* spp.) for sites (forest stands) in a

higher deer area (private hunt club, 29 sites) and a lower deer area (State Forest, 31 sites).

### 2.3.2. Maximum deer browsing and shrub canopy height

Since our goal was to establish the maximum, rather than average, reach of browsing deer, we considered maximum value and high quantile values (e.g. 90th percentile) to be more relevant than means. Thus, we summarized deer browsing maximum height values for seedlings in the PLANTED study with quantile box plots. For shrub canopy height data, we developed a plot of maximum shrub canopy height for gap plots vs. harvest gap size for data pooled from the two sites comprising the PLANTED study (Walters et al., 2014, 2016, Table 1). Based on our biological expectation that shrub height would reach a high light asymptote, we fitted potentially appropriate model forms (e.g. non-linear Michaelis-Menton, Mechanistic Growth, knotted spline) and settled on the Mechanistic Growth model based on AICc scores. Based on this model fit we restricted data to  $> 800 \text{ m}^2$  gap size and examined shrub height distribution quantiles.

### 2.3.3. Shrub, deer, and light effects on planted seedlings

Preliminary mixed least squares height models and parametric survival models for planted seedlings from the PLANTED study revealed *GAP LIGHT* (fitted with knotted splines when supported by AIC scores), *SHRUB*, and *DEER* effects that varied among species in strength and in form for *GAP LIGHT* (data not shown). Given these results, we separated data into species  $\times$  treatment (i.e. *SHRUB*, *DEER*, *DEER* + *SHRUB*, *CONTROL*) combinations for further analyses and presentation of height growth and survival in this report. We included *GAP LIGHT* in models where it was relevant to our goals and for treatments where it was generally a significant effect among species.

All height data are for seedlings from the PLANTED study. We present height data three ways: at a single point in time, over time, and across *GAP LIGHT*. For point in time measurements, we focused on seedlings that had spent five years in treatments. Our rationale was that all species could be compared using five year data (as we did not have six year heights for three species in fenced treatments due to fence failure and subsequent deer browsing). For height over time we present median and maximum values for all live seedlings (no *GAP LIGHT* effects) over six years, only in the *DEER* + *SHRUB* treatment. For *GAP LIGHT* effects we fitted seedling height as a function of *GAP LIGHT* with least squares regression for each treatment combination. We started with linear fits, and then added a three-knot spline, then a four-knot spline if supported by AIC scores and biological expectations (e.g. lines with two maxima were not allowed). Given these criteria, most final models included a three-knot spline effect for *GAP LIGHT*.

All survival analyses are for seedlings from the PLANTED study. As a general overview of our approach to survival (presented here as mortality) analysis, we used parametric survival analysis to develop separate models for each species by treatment combination. Seedlings that were thinned from the experiment or remained alive at the final census were right censored in the models. For each model, Weibull, log-normal, exponential, Frechet, and log-logistic distributions were evaluated, with the final model chosen based upon AICc scores. For whatever factor or combination of factors were considered as predictors, effect significance was assessed with likelihood ratio tests (i.e. compares full model vs. model not containing effect of interest). With final models, mortality estimates with 95% confidence intervals were generated for the period desired (see below).

We developed different parametric survival models for PLANTED seedling data to address different goals. To examine mortality trajectories over time we developed model estimates of mortality, by year, for the *DEER* + *SHRUB* treatment. We evaluated evidence of negative height-dependent tree seedling mortality from deer browsing and shrub competition by using seedling height measured in autumn 2012 (two years in treatments) to predict mortality for three years following height measurement (autumn 2012 - autumn 2015). Given that *GAP*

*LIGHT* is collinear with seedling height (confirmed in preliminary models) and can impact mortality independently or interactively with deer and shrub effects, we included *GAP LIGHT* (with splines if supported by AIC scores) and 2012 height in our mortality models, and report model results and 95% confidence intervals at the experimental mean *GAP LIGHT* of 29.5%. In addition, because preliminary models revealed especially strong effects of light on height-dependent mortality for *SHRUB*, we also developed model estimates of mortality vs. height for *SHRUB* at 10% and 40% *GAP LIGHT* for a subset of representative species.

We used histograms to examine patterns in the PLANTED study of sapling recruitment (i.e. height  $> 2 \text{ m}$  tall after six years in treatments), mortality, and living seedlings  $< 2 \text{ m}$  tall over *GAP LIGHT* categories in species by treatment combinations. We chose histograms instead of statistical modelling for two reasons. First, statistical analysis of sapling recruitment is compromised for some treatment combinations because we had to thin some individuals less than 2 m tall to prevent crowding earlier in the experiment, and some of these could have become sapling recruits by the end of the experiment. Second, preliminary logistic recruitment models for some species by treatment combinations by *GAP LIGHT* did not converge when sapling recruitment was very low (e.g. one or two individuals per treatment combination), yet even low rates of recruitment are ecologically relevant. Concentrating on the *DEER* + *SHRUB* treatment, as it represents realistic conditions over large extents of forested land, we evaluated differences in species recruitment (after six years in treatments) with the previously described histograms. For species without recruits after six growing seasons in treatments, we assessed the potential for future recruitment from height growth and mortality patterns over time. We used these data to develop three sapling regeneration niche groups (see Results).

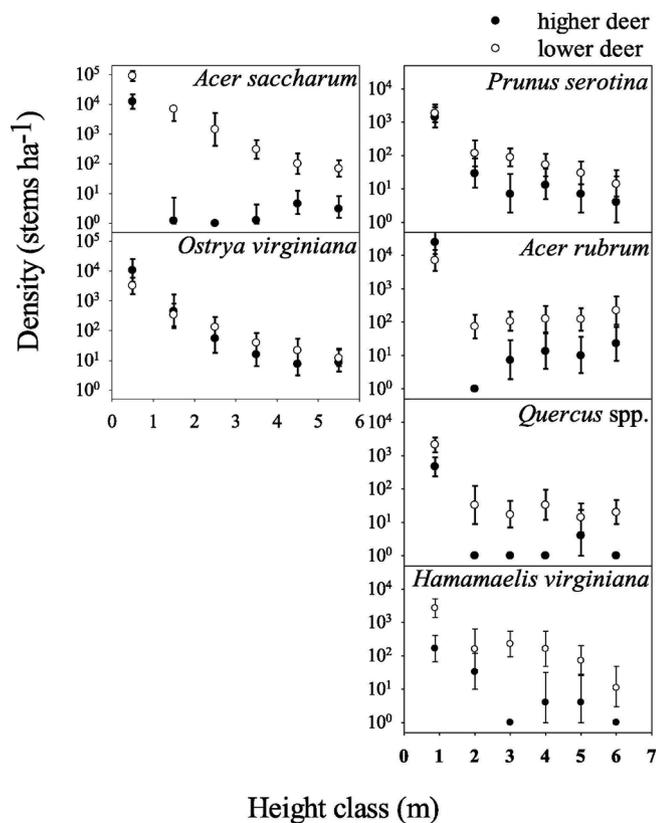
We used Principal Components Analysis (PCA, JMP multivariate platform) as an aid to develop a more general understanding of sapling recruitment niches and their underlying growth and survival properties among our 16 tree species. Our PCA included seven species-based properties and indices based on height growth and mortality responses to PLANTED study treatments (described in Results) with the goal of identifying which combinations of species properties were associated with each sapling recruitment niche group. Preliminary analyses of variables to test linear assumptions of PCA included visual examination of correlation matrices, comparing Pearson vs. non-parametric Spearman's correlations, and evaluating linear vs. non-linear knotted spline models with AICc. Among bivariate correlations (21 total) analyses confirmed that the assumption of linearity was met.

## 3. Results

### 3.1. Is the height structure of juvenile tree populations consistent with a sapling recruitment bottleneck caused by deer browsing?

Among harvest gaps in northern hardwood stands (NH\_NAT study, Table 1), we found starkly different juvenile tree densities by height class for browsing-sensitive *A. saccharum* between more northerly regions with deeper snow and lower deer densities ( $< 10 \text{ km}^{-2}$ ) and more southerly regions with shallower snow and higher deer densities ( $> 20 \text{ km}^{-2}$ , Matonis et al., 2011) (Fig. 1). Particularly striking was the four orders of magnitude decline in density from the 0–1 m ( $12,334 \text{ ha}^{-1}$ ) to 1–2 m height class ( $1.2 \text{ ha}^{-1}$ ) and the persistence of low densities in taller classes ( $< 5 \text{ ha}^{-1}$  in any one class  $> 1 \text{ m}$  tall) at higher deer densities. In contrast, densities by height class differed little between high and low deer density areas for browsing-insensitive *O. virginiana*, with 95% confidence intervals overlapping considerably for every height class.

Tree stem densities in *Populus* spp. forest understories (POP\_NAT study, Table 1) also fell between shorter (0.25–1.5 m) and taller (1.5–2.5 m) height classes, with sharper declines in the higher deer

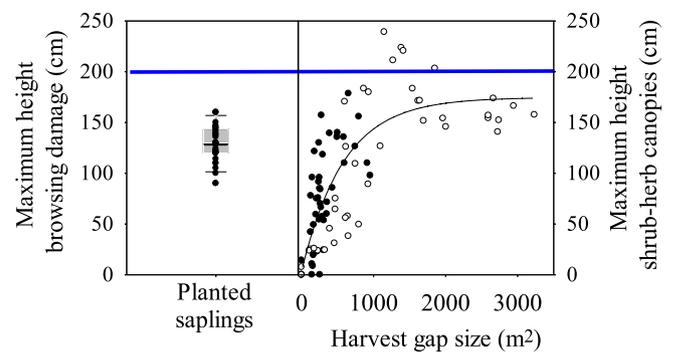


**Fig. 1.** Estimated tree stem densities (with 95% confidence intervals) by height class. Left column: browsing-sensitive *Acer saccharum* and browsing-insensitive *Ostrya virginiana* in northern hardwood forest gaps (NH\_NAT study) in areas characterized by higher deer (estimated for 10th percentile northing of our study area) and lower deer (90th percentile of northing).  $N = 59$  sites. Right column: understory woody stem densities on sites dominated by *Populus* spp. (POP\_NAT study) at higher deer browsing pressure (11 deer  $\text{km}^{-2}$ ,  $n = 31$ , open circles) vs lower deer browsing pressure (6.8 deer  $\text{km}^{-2}$ ,  $n = 29$ , closed circles). A value of 1 was added to all graphed values so that zero could be shown on a log-y axis (i.e. at  $\log_{10}^0$  the actual value = 0).

density region (Fig. 1). Similar to patterns in northern hardwood gaps, differences in species sensitivity to deer browsing led to changes in tree composition between size classes in *Populus* spp. understories; e.g., with increasing height, the relative importance of browsing-sensitive *A. rubrum* decreased while the relative importance of browsing-insensitive *Prunus serotina* Ehrh. increased (Fig. 1). Furthermore, similar to patterns in northern hardwood forest gaps, the diminished density of tree stems in higher deer areas persisted into height classes taller than browsing deer can physically reach, possibly reflecting historical legacies of deer browsing pressure (Walters et al., 2020).

### 3.2. Can a critical height threshold for sapling recruitment be identified from maximum shrub canopy height, maximum deer browsing height, and patterns of height-dependent juvenile tree mortality?

Data from the planted seedling experiment (PLANTED study, Table 1) indicated maximum browsing heights of 160 cm (90th percentile and maximum). Maximum shrub layer canopy height and percent cover increased with harvest gap size and GAP LIGHT, ultimately plateauing in gaps  $> 800\text{--}1000\text{ m}^2$  and  $> 20\text{--}30\%$  GAP LIGHT (Fig. 2 for gap size vs. height, Supplementary Materials, Fig. S1 for other relationships). Although *Rubus* spp. generally dominated the shrub layer in the two stands we examined, *Sambucus* spp. shrubs exceeding 200 cm in height dominated a few harvest gaps. Restricting our data set to gaps  $> 800\text{ m}^2$ , the 90th percentile of shrub canopy height was 221 cm overall and 183 cm excluding gaps with *Sambucus*. Shrub layer



**Fig. 2.** Left panel: box plots (median, 25th – 75th percentile (shaded), 10th – 90th percentile (outer bars) and data for maximum height of browsing damage on 7–8 year old planted saplings ( $n = 36$  saplings). Right panel: maximum height of shrub layer vegetation dominated by *Rubus* spp. vs. harvest gap size (gap-centered plots) measured at the two experimental sites (closed and open circles). Model fit  $R^2 = 0.70$ ,  $P < 0.0001$ . All data are from the PLANTED study (Table 1).

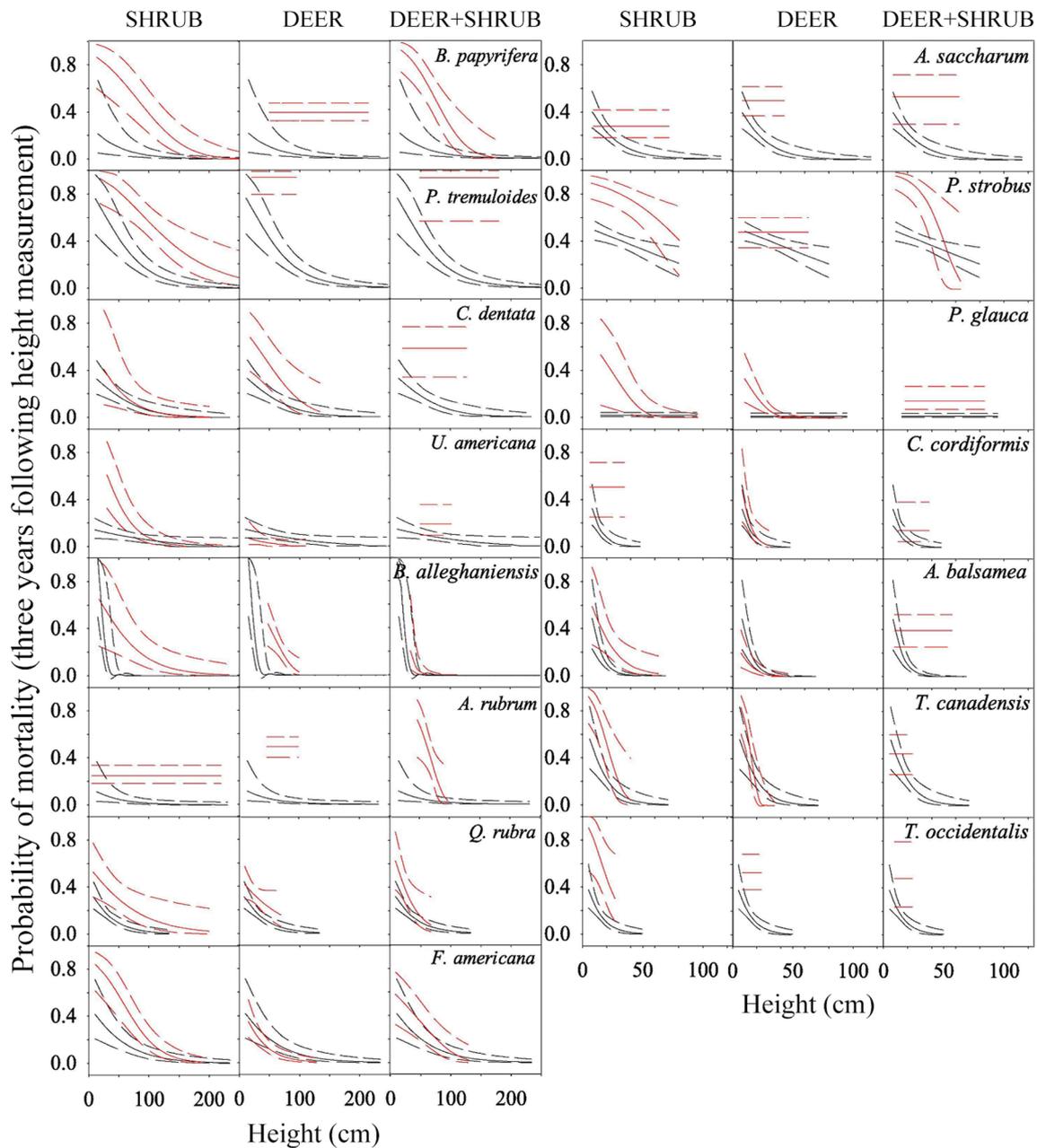
coverage in gaps  $> 800\text{ m}^2$  was high (median = 100%, 90th percentile = 127%) and dominated by *Rubus* spp. (median = 77.5%, 90th percentile = 100%) (Fig. S2).

In our PLANTED study, we predicted shrub layer competition and deer browsing pressure would have negative height-dependent mortality effects on tree seedlings. However, negative height-dependent mortality was widespread among species in the CONTROL treatment (Fig. 3), due to height-dependent mortality agents we did not control or account for; e.g. soil resource deficiencies, disease, and mechanical damage. Given these patterns, we interpret SHRUB and DEER effects on height-dependent mortality as mortality in excess of mortality in CONTROL.

Among species, there were examples of negative height dependent mortality from DEER, SHRUB, and DEER + SHRUB treatments, but SHRUB had the most consistent effects (12 of 15 species, Fig. 3). In SHRUB, nearly all mortality estimates were higher (i.e. non-overlapping 95% confidence intervals) than for CONTROL seedlings at lesser heights (e.g. 50 cm tall), then converged for the treatments at greater heights (e.g. 100–200 cm tall, Fig. 3). Compared to SHRUB effects at experimental mean GAP LIGHT of 29.5%, negative height-dependent mortality effects were larger at 40% GAP LIGHT (i.e. greater separation between mortality vs. height functions for SHRUB and CONTROL treatments), where shrubs are denser, and negligible at 10%, where shrub canopies are sparse (Fig. S2). Mortality in DEER and DEER + SHRUB treatments was consistently higher than in CONTROL among species. However, these treatments less consistently showed height dependence than SHRUB. Instead, DEER and DEER + SHRUB treatments show that chronic browsing maintains seedlings at short stature. Prevented from being able attain heights sufficient to reduce and escape deer-dependent mortality, seedlings trapped at short stature continue to have high mortality rates. Collectively, information on maximum *Rubus* spp.-dominated shrub canopy height, maximum deer browsing height, and height dependent mortality from shrubs and deer indicate a height threshold of approximately 1.6–2 m above which saplings escape the effects of both shrub competition and deer browsing. Hereafter, we conservatively define this height threshold as 2 m. Saplings of this height should have the upper portions of their crown beyond shrub shading and browsing effects. Hereafter, saplings transcending 2 m in height are termed sapling recruits.

### 3.3. How do shrub competition, deer browsing pressure, and light availability interact to shape interspecific sapling recruitment niches?

Species varied appreciably in several height and survival indices potentially related to their relative abilities to become sapling recruits



**Fig. 3.** Modeled parametric survival analysis estimates (solid lines) and 95% confidence intervals (hatched lines) of mortality as a function of height for seedlings of 15 species (models did not converge for *J. nigra*) from the PLANTED study. Heights are for three-year old seedlings in treatments for two growing seasons. The mortality interval is for the three years following height measurements. Functions in red correspond to treatments on column headers, while those in black are for the CONTROL treatment. For treatments in which harvest gap light availability affected mortality independently of height, light was retained in the model and height estimates are shown at the mean light level across all plots (29.5% open sky). The horizontal lines shown for many of the species by treatment combinations are for cases where the  $P > \chi^2$  value for height was  $> 0.10$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Table 2). Height growth potential (i.e. height vs. GAP LIGHT maxima in CONTROL, Fig. S3) ranged from ~0.4 m for *T. occidentalis* to 4.3 m for *B. papyrifera* (Table 2). Except for CONTROL seedlings, GAP LIGHT effects on height were variable in strength and form among species (data not shown). Reducing data to mean values (i.e. without GAP LIGHT in models) greatly simplifies presentation and sufficiently captures relevant treatment effects. Considering mean values, SHRUB, DEER, and DEER + SHRUB treatments diminished seedling height relative to CONTROL (Table 2, Fig. S4). SHRUB negative impacts were greatest on an absolute scale for *A. rubrum* (-66 cm) and on a relative scale for *P. strobus* (45% reduction). DEER effects were generally greater

than SHRUB effects, but were variable among species (e.g. *P. tremuloides* and *B. alleghaniensis*, 83–84% height reduction in DEER relative to CONTROL vs. *P. glauca*, 2% height increase) (Table 2, Fig. S4). Seedlings of several species either had near zero growth or negative growth over the last three years in the DEER treatment ( $\Delta$  height, Table 2). Compared to DEER and SHRUB effects, DEER + SHRUB effects indicated that shrubs partially ameliorate negative deer impacts on height growth for some species, most of which were among the fastest growing (Fig. S4, and see further).

Mortality varied among treatments, with mean values across species (GAP LIGHT not in models): 38% in CONTROL, 61% in DEER, 54% in

**Table 2**

Species growth and survival indices from PLANTED study and used as variables in PCA (Table 3, Fig. 5). Height indices are for five years in treatments and mortality for six years. Species are arranged, top to bottom, from highest to lowest maximum height in the CONTROL treatment (Height vs. GAP LIGHT maxima, Fig. S3). Other height indices are treatment means (Fig. S4).  $\Delta$  height is for last three years of experiment. Deer mortality is DEER – CONTROL (Fig. S5), shrub mortality is SHRUB – CONTROL @ 40% GAP LIGHT (data not shown) and shade mortality is Mortality @ 3% GAP LIGHT – (mortality vs. GAP LIGHT minima) in CONTROL (Fig. S6).

Species	Recruitment group	Max height CONTROL (cm)	Height CONTROL (cm)	Height SHRUB (cm)	Height DEER ( $\Delta$ height) (cm)	Mortality DEER (%)	Mortality SHRUB (%)	Mortality Shade (%)
<i>Betula papyrifera</i> Marshall	High light	434	277	249	50 (-12)	14	26	40
<i>Populus tremuloides</i> Michx.	High light	401	251	224	41 (-9)	22	40	60
<i>Betula alleghaniensis</i> Britton	High light	357	227	174	39 (-3)	15	30	40
<i>Castanea dentata</i> <sup>#</sup> (Marsh.) Borkh.	Broad	357	194	142	60 (0)	15	18	6
<i>Ulmus americana</i> L.	Broad	315	172	152	50 (8)	12	26	0
<i>Juglans nigra</i> <sup>#</sup> L.	Broad	305	242	271	151 (103)	29	29	39
<i>Acer rubrum</i> L.	Nowhere	275	159	93	31 (-7)	44	51	61
<i>Quercus rubra</i> L.	Nowhere	216	116	71	30 (4)	28	40	27
<i>Fraxinus americana</i> L.	Broad	205	124	128	71 (10)	0	25	28
<i>Acer saccharum</i> Marshall	Nowhere	153	86	53	24 (1)	6	21	29
<i>Picea glauca</i> (Moench)Voss	Broad	135	86	64	88 (72)	10	19	4
<i>Pinus strobus</i> L.	Nowhere	113	62	36	51 (43)	6	34	17
<i>Abies balsamea</i> L. (Mill.)	Nowhere	69	45	28	35 (14)	17	23	2
<i>Carya cordiformis</i> <sup>#</sup> (Wanenh.) K. Koch	Broad	59	40	30	27 (12)	13	29	19
<i>Tsuga canadensis</i> (L.) Carriere	Nowhere	57	33	22	25 (0)	9	19	0
<i>Thuja occidentalis</i> L.	Nowhere	42	33	21	19 (-2)	7	22	0

<sup>#</sup> It indicates the experiment location was outside of the species' natural range.

SHRUB and 64% in DEER + SHRUB (Fig. S5). Mortality also varied appreciably among species within treatments (e.g. from 25% for *P. glauca* to 89% for *T. occidentalis* in DEER + SHRUB (Table 2, Fig. S5)). We generated an index of mortality from shrub competition at 40% light, where the shrub layer was dense, as mortality @ 40% light (SHRUB – CONTROL) (Fig. S6 for CONTROL, SHRUB not shown). For this index, mortality from the shrub layer ranged from 18% for *C. dentata*, to 51% for *A. rubrum* (Table 2). Our index of mortality from deer browsing (Mortality (DEER – CONTROL), Fig. S5) ranged from 7% mortality for *T. occidentalis* to 44% for *A. rubrum*. Shade mortality (CONTROL (mortality @ 3% light – light-dependent mortality minima) Fig. S6) ranged from 0% for *T. occidentalis* and *T. canadensis* to 61% for *P. tremuloides* and *A. rubrum* (Table 2).

We examined the proportion of seedlings in the PLANTED study that were sapling recruits (i.e. height > 2 m tall), dead, or living and < 2 m tall after six years by treatment and GAP LIGHT category. In CONTROL, 12 of 16 species produced sapling recruits after six years (Fig. S7) with only those of lowest height growth potential (Table 2) not producing any recruits. Recruitment was greater in higher than lower GAP LIGHT in CONTROL; no species produced sapling recruits in < 10% light, where mortality was high and/or height growth potential was low. Due to lower growth and higher mortality, fewer species produced recruits in SHRUB (10 species) and DEER (5) than in CONTROL. Most recruits in DEER were of browsing-insensitive species *P. glauca* and *J. nigra* (Fig. S7).

In DEER + SHRUB (Fig. 4), seven species produced sapling recruits, with the three species with greatest height growth potential (i.e. browsing-sensitive *B. papyrifera*, *B. alleghaniensis*, and *P. tremuloides* (Table 2)) producing recruits only in larger, high-light gaps where shrub competition was dense (Fig. 4). Furthermore, all seven species either produced more recruits or recruited solely in DEER + SHRUB as compared to DEER (Fig. S7, Fig. 4). Species not restricted to high GAP LIGHT for sapling recruitment in DEER + SHRUB included browsing-insensitive species of moderate-to-high height growth potential including *J. nigra*, *F. americana*, and *U. americana*, as well as fast-growing, browsing-sensitive *C. dentata* (Table 2, Fig. 4).

In addition to the seven species that recruited saplings after six years in DEER + SHRUB, others may recruit in the future. We extrapolated

six-year trends of height growth and mortality to predict which other species would likely produce sapling recruits in the future (Fig. 4). At only 25% mortality, a maximum height of 168 cm after six years, and maximum height increasing steadily over time, some *P. glauca* individuals are virtually assured of becoming saplings recruits in the future (Fig. 4, Table 2). In addition to *P. glauca*, *C. cordiformis* is the only other species that may produce recruits that has not already done so, though its potential for doing so is marginal. After six years, 51% were dead and the maximum height was 101 cm (and increasing over time). Extrapolating maximum height and average mortality trajectories, the largest individuals could reach 200 cm at a population mortality rate of 93%. Other species without sapling recruits after six years were *A. rubrum*, *Q. rubra*, *A. saccharum*, *P. strobus*, *A. balsamea*, *T. canadensis*, and *T. occidentalis*. All of these species have some combination of high mortality, short stature, and slow growth rates that makes sapling recruitment unlikely in the face of deer browsing pressure and shrub competition in this experiment (Fig. 4).

Based on patterns of sapling recruitment and potential for future sapling recruitment in DEER + SHRUB, we classified species into three recruitment niche groups (Table 2). The groups are (1) *High Light*, in which recruitment occurred only in large, high light gaps, (2) *Broad*, in which recruitment occurred or will likely occur over a broad range of gap sizes, and (3) *Nowhere*, in which sapling recruitment is unlikely to occur in gaps of any size.

In a PCA that included height growth and mortality indices as variables (Table 2) and species and recruitment niche groups as supplementary variables, Component 1 (40.1% of variance) captured positive associations between height growth potential, mean height in SHRUB, and mortality from shrub competition, deer browsing, and shade (Fig. 5, Table 3). High Component 1 values for the *High Light* group partly separates it from the *Nowhere* and *Broad* groups. *High Light* species can recruit in large, high-light gaps where they grow fast, but have high mortality from shrub competition, deer browsing, and shade. Conversely, Component 1 generally indicates that *Broad* and *Nowhere* species have lower height growth potentials, lower realized height growth when competing with shrubs, and lower shade mortality than *High Light* species. Component 2 (30.1% of variance) captures deer effects and separates *Nowhere* and *Broad* groups. Relative to the *Nowhere*

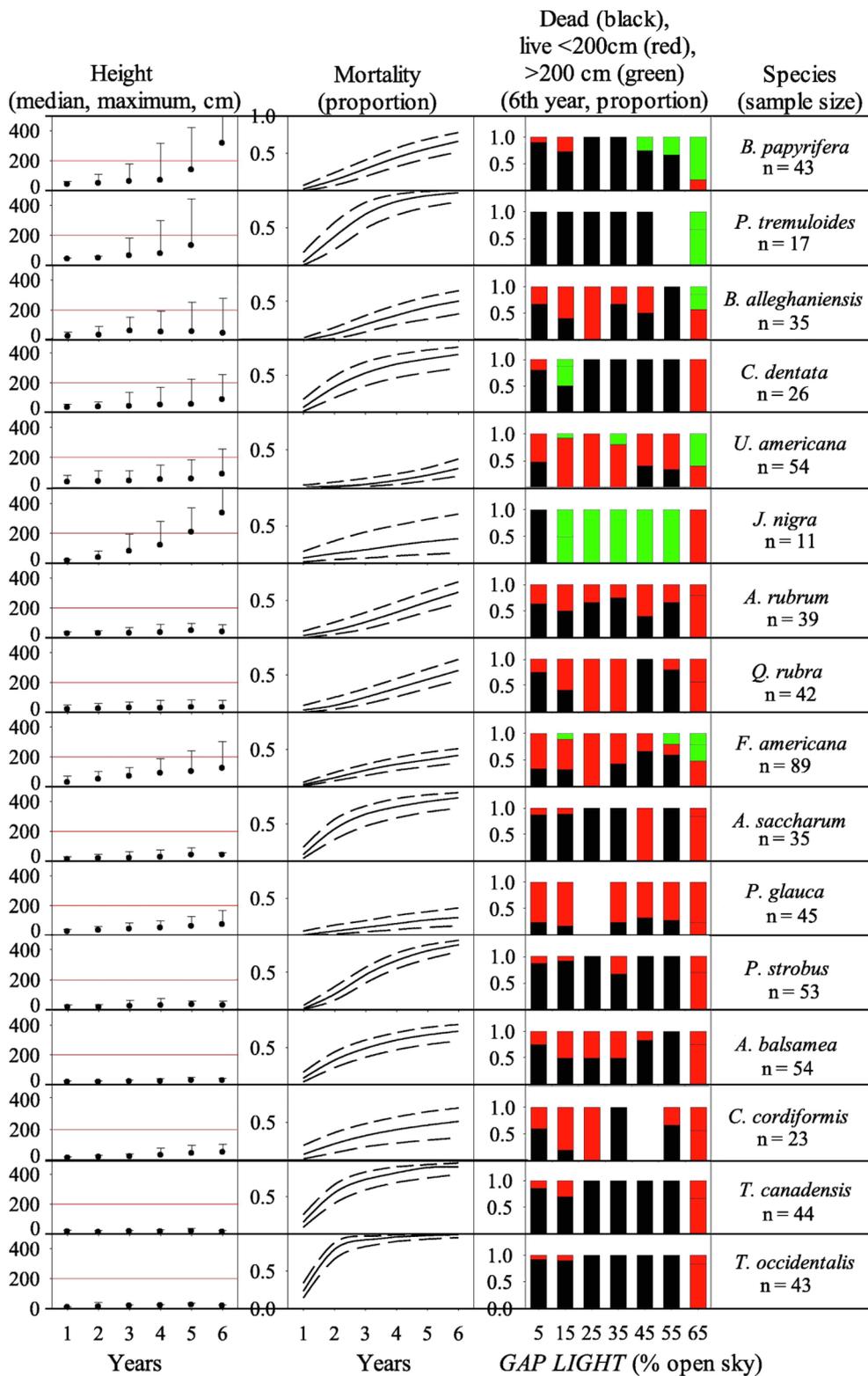
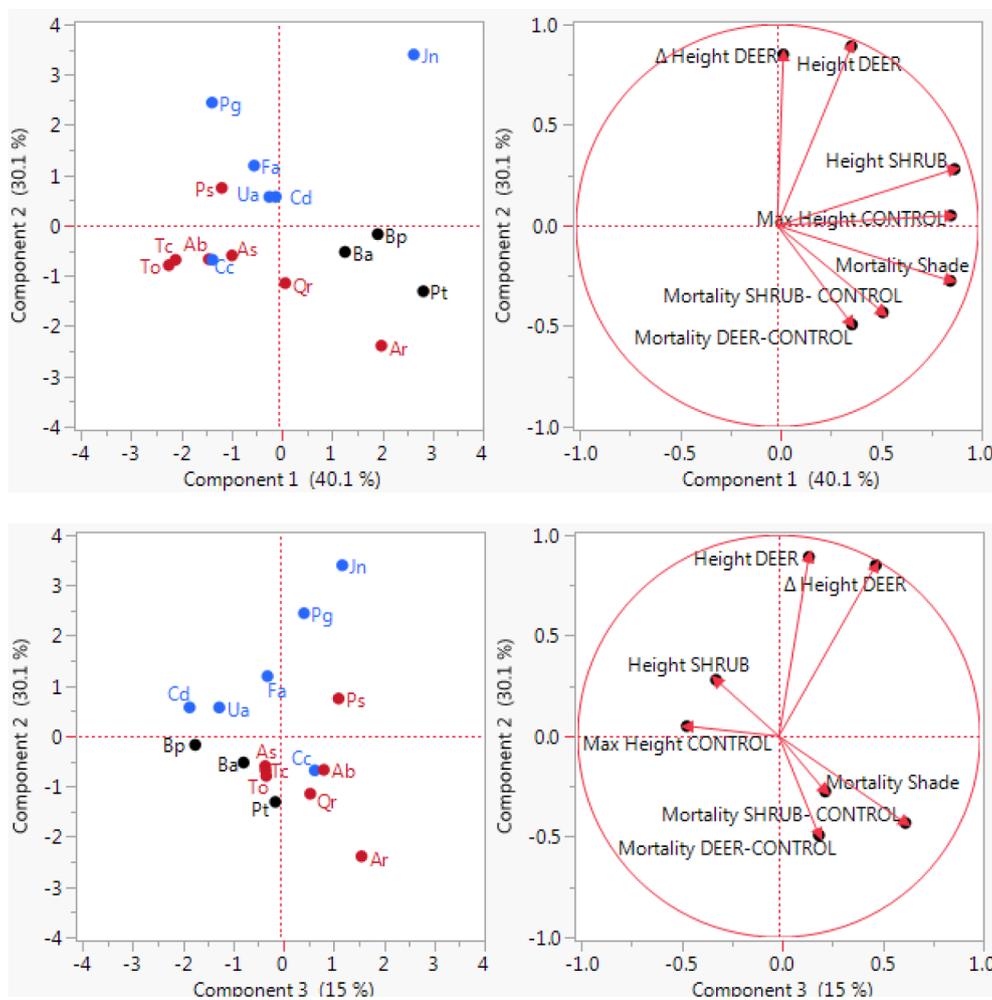


Fig. 4. For seedlings from the PLANTED study in the DEER + SHRUB treatment: Column 1) median and maximum height over time (years); Column 2) mortality estimates (with 95% CI) over time; Column 3) Proportion of seedlings by species (rows), treatment (column header) and GAP LIGHT categories (x-axis label) reaching heights > 2 m (green), < 2 m (red), or dead (black) after six years. “n” indicates the number of seedlings used for each histogram. Species are ordered top-to-bottom by descending height growth potential (Table 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

group, height growth and mortality for *Broad* group species is generally less impacted by deer browsing pressure. Component 3 captures residual variation in height growth potential (and height in *SHRUB*) vs. mortality from shrubs and  $\Delta$  height due to deer. Component 3 helps to further separate species into *High Light* and *Nowhere* groups. This separation is greatest for *A. rubrum*, and its responses serve to illustrate the fate of *Nowhere* species. With relatively low height growth potential

and higher mortality from shrubs than needed to overcome shrub competition in large canopy gaps, combined with negative impacts of deer browsing on height growth and mortality precluding its recruitment in smaller gaps, *A. rubrum* and other species in the *Nowhere* group are without a sapling recruitment niche in forests characterized by high deer populations and dense shrub layers.

Three species deviated somewhat in PCA clustering by recruitment



**Fig. 5.** A score plot (left) and loading plot (right) for the first three principal components from Principal Components Analysis. A loading matrix for the first four principal components from this analysis is provided in Table 3. Species acronyms are for their Latin binomials (Table 2). The color of species data points are for a priori assigned sapling recruitment groups (i.e. black = High Light, blue = Broad, red = Nowhere). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

niches. *J. nigra*, one of three species planted outside its current range (*C. cordiformis* and *C. dentata* being the other two), had high growth potential, similar to species in the High Light group, but with height growth little affected by deer, similar to species in the Broad group. *C. cordiformis* barely met the criteria for placement in the Broad group rather than Nowhere group and, unsurprisingly, clustered firmly with species in the Nowhere group. *P. strobus* is distinct among Nowhere species in exhibiting positive height growth under deer browsing pressure. More than any other species, *P. strobus* growth and mortality was much more sensitive to shrubs than deer (Fig. 6, SM 3), suggesting it could be a member of the Broad group in habitats with lower shrub competition (e.g. less-fertile sites).

#### 4. Discussion

##### 4.1. Shrub competition and deer browsing impose species-specific, height-dependent bottlenecks to tree recruitment

The height structure of juvenile tree populations, maximum heights of deer browsing and the *Rubus* spp.-dominated shrub layer, and negative height-dependent effects of shrubs and deer on juvenile tree mortality collectively indicate species-specific bottlenecks to sapling recruitment in forests characterized by dense shrub layers and high deer populations. Saplings escape deer and shrub effects as they grow taller than 2 m, above which trees have a much greater chance of reaching

**Table 3**

Loading matrix for PCA (Fig. 5). Loading values are the correlations between the original variables and the unit scaled components (i.e. Component 1, Component 2, etc.). Loadings > |0.3| are in bold.

Original variable	Component 1 (2.810)	Component 2 (2.104)	Component 3 (1.049)	Component 4 (0.755)
Height SHRUB	<b>0.8814</b>	0.2807	-0.3128	0.1197
Max Height CONTROL	<b>0.8626</b>	0.0503	-0.4577	-0.1116
Mortality Shade	<b>0.8601</b>	-0.2745	0.2304	-0.1777
Height DEER	<b>0.3683</b>	<b>0.8921</b>	0.1487	0.0561
Δ Height DEER	0.0296	<b>0.8509</b>	<b>0.4816</b>	0.1327
Mortality SHRUB-CONTROL	<b>0.5243</b>	-0.4309	<b>0.6288</b>	-0.3116
Mortality DEER-CONTROL	<b>0.3711</b>	-0.4915	0.1984	<b>0.7610</b>

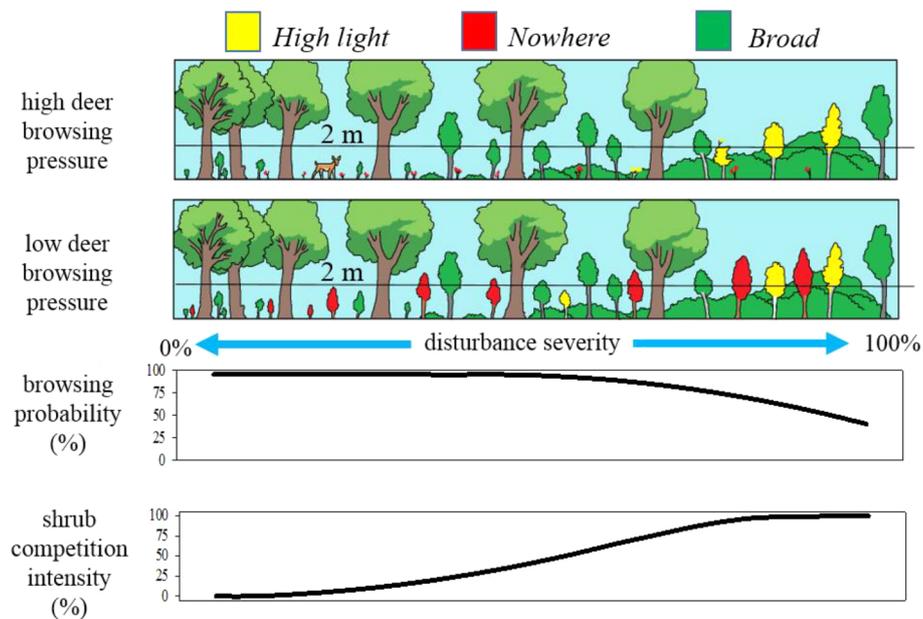


Fig. 6. Conceptual diagram of species sapling recruitment group (i.e. *High Light*, *Broad*, *Nowhere*) niches as constrained by browsing probability and shrub layer competition intensity over a canopy disturbance severity gradient.

maturity. Large differences in composition and density between  $< 2$  m and  $> 2$  m height classes indicate that future forest dynamics cannot necessarily be predicted from trees  $< 2$  m tall.

Other regional studies of juvenile tree population structure (Bradshaw and Waller, 2016, Russell et al., 2017, Westfall and McWilliams, 2017, Reuling et al., 2019) and maximum deer browsing height (140 cm, Saunders and Puettmann, 1999) suggest that deer browsing pressure bottlenecks to sapling recruitment, similar to what we observed, are widespread in Eastern North America. Furthermore, similar sapling recruitment bottlenecks from high ungulate populations may be common elsewhere (Ramirez et al., 2018), including Western Europe (Perea et al., 2014, Ameztegui and Coll, 2015), Fennoscandia (Persson et al., 2000), Japan (Takatsuki, 2009), and New Zealand (Forsyth et al., 2010).

Similarly, *Rubus* spp. form dense, tree regeneration-stymieing shrub layers following forest canopy disturbance in many temperate forests in North America and worldwide (Metzger and Tubbs, 1971, Harmer et al., 2005; Donoso and Nyland, 2006, Kern et al., 2012, Balandier et al., 2013, Prévost and Charette, 2015), and dense layers can persist  $> 10$  years following partial stand harvest, potentially leading to extended delays in sapling recruitment (Kern et al., 2013, Widen et al., 2018). Importantly, however, *Rubus* spp. and other shrub effects on tree regeneration are not always negative and/or persistent (Donoso and Nyland, 2006). Effects could vary with several factors, including disturbance size and shrub density (Widen et al., 2018, this study), shrub height vs. tree height structure (Walters et al., 2016, Widen et al., 2018), positive non-resource related effects outweighing negative competitive effects (e.g. protection from deer browsing, Walters et al., 2016), soil resource impacts on shrub density (Willis et al., 2016), and competitive vs. facilitative resource-related interactions (Montgomery et al., 2010). However, in this study we consistently found negative effects of *Rubus* spp. on tree seedlings that dissipated when trees reached the height of *Rubus* spp. shrub canopies, suggesting competition for light is paramount (Horn, 1971, Schwinning and Weiner, 1998).

A critical height threshold of approximately 2 m for sapling recruitment is specific to landscapes characterized by *Rubus* spp.-dominated shrub canopies and white-tailed deer browsing pressure. Critical height thresholds for sapling recruitment are likely common in other systems, with specific threshold heights defined by the identities of

dominant local shrub and ungulate species. For example, dense shrub layers can range appreciably ( $< 1$  m to  $> 4$  m in height, Royo and Carson, 2006), as can maximum browsing heights (e.g. 1.3 m for roe deer (*Capreolus capreolus*) (Chianucci et al., 2015) to 3.05 m for moose (*Alces alces*) (Andreozzi et al., 2014). Identification of height thresholds for sapling recruitment could improve our understanding, prediction, and management of vegetation dynamics for many forested ecosystems.

#### 4.2. How do shrub competition, deer browsing pressure, and light availability interact to shape interspecific sapling recruitment niches?

Recent studies in the temperate forests of Eastern North America have revealed that the expected effects of canopy disturbance severity on species-specific sapling recruitment dynamics (Runkle, 1981, Shugart, 1984, Pacala et al., 1996) can be overridden by the additive effects of deer browsing and/or shrub layers (Beckage et al., 2000, Royo and Carson, 2006, Kern et al., 2012, Nuttle et al., 2013). In addition, shrubs, deer, and light have been shown to have complex interacting effects on sapling recruitment (Horsley and Marquis, 1983, Walters et al., 2016, Laurent et al., 2017). In this study, we confirm that deer can override the positive effects of harvest gaps on sapling recruitment for several browsing-sensitive species and that shrub layer competition can override the benefits of increased gap light to recruitment for subordinate stems of slower growing species. In addition, we confirm for older sapling recruits what Walters et al. (2016) found for seedlings; namely that shrubs, deer, and harvest gap size interact, with shrubs having facilitative effects on sapling growth for faster growing species in the face of deer browsing pressure in large harvest gaps where shrubs are dense (Fig. S4). In addition, we confirmed that the positive effects of shrubs on sapling growth were associated with reduced probability of browsing (Fig. S8).

Our results suggest a conceptual model of forest dynamics in the temperate forests of Eastern North America that recognizes how covariation in shrub layer competition, deer browsing pressure, and light availability drive differences in tree species sapling recruitment niches (Fig. 6). Essentially, species respond uniquely over a gradient characterized by increasing shrub competition and decreasing deer browsing pressure as canopy tree disturbance severity (e.g. harvest gap size) increases, with species roughly falling into three regeneration niche groups based on their height growth potential as well as their

growth and mortality rates as affected by shrub competition, deer browsing, and shade.

Our three groups, *High Light*, *Broad*, and *Nowhere* apply to sapling recruitment in forests characterized by both high deer browsing pressure and dense shrub layers in canopy openings (Fig. 6). The *High Light* group consists of species capable of rapid height growth that are intolerant of shade, shrub competition, and deer browsing. These species can recruit saplings only in high severity canopy disturbances (e.g. large harvest gaps) (Fig. 4). In these environments, they are partially protected from deer browsing by shrubs, but need to quickly escape browsing deer and competition from the ascending shrub canopy that develops rapidly following disturbance. The *Broad* group includes species with a broad range of shade tolerances, but with most species slower-growing and more browsing-insensitive than those in the *High Light* group. They are characterized by their abilities to maintain positive height growth at manageable mortality rates under deer browsing pressure. In forests with high deer populations, their regeneration strategy is to establish as advance regeneration, then recruit following canopy disturbance over a relatively broad range of disturbance severities (i.e. harvest gap sizes/light availabilities). In addition to our study species, other species currently dominating sapling recruit populations in the understories of forests with high deer populations such as *O. virginiana* and *Fagus grandifolia* Ehrh. likely fall into this group (Rossell et al., 2005, Matonis et al., 2011, Bose et al., 2017). Species in the *Nowhere* group don't grow fast enough to regenerate from seed following disturbance in large gaps. Most are intolerant of shrub competition and have high mortality rates and negligible to negative height growth rates in the face of deer browsing pressure, leading to very low probabilities of sapling recruitment. Their regeneration strategy, like the *Broad* group, is by establishing populations of advance regeneration that subsequently respond to canopy disturbance. However, species in the *Nowhere* group cannot maintain advance regeneration of sufficient stature to compete with shrubs following canopy disturbance due to heavy browsing pressure in forest understories. Many of the species identified as having significant regeneration challenges in the forests of Eastern North America fall into this group, including *Q. rubra*, *A. saccharum*, *T. occidentalis* and *T. canadensis* (Matonis et al., 2011, Bradshaw and Waller, 2016, Westfall and McWilliams, 2017).

We believe it's important to note that our recruitment groups are somewhat arbitrary and are based on limited data from a relatively narrow geographic extent and set of experimental conditions. It's also clear that many other factors besides light, shrubs, and deer drive forest dynamics in northern temperate forests (Webster et al., 2018). However, the framework we have developed is generally supported by sapling recruitment patterns across Eastern North American forests (see previous paragraph). We suggest that it is useful for conceptualizing and generalizing forest dynamics and can serve as a template for further necessary empirical work.

## 5. Management implications

We suggest three applications of our results for forest management: (1) the assessment of tree regeneration success should be limited to sapling recruits, (2) improving forest tree diversity, resilience, and sustainability may hinge on changing harvesting paradigms, rapid tree establishment, and/or temporary reductions in deer populations, and (3) individual species and niche sapling recruitment group results provide guidance for climate adaptation and diversity enrichment planting efforts.

Although regeneration surveys of small seedlings conducted soon after harvest (e.g. 2–4 years) may be useful in terms of assessing the timely stocking of tree seedlings, such surveys can be poor predictors of future canopy composition (Leak, 2007, this study). Some operational stocking guides used by forest managers explicitly consider minimum height and “free to grow” (i.e. sapling recruit) standards for crop trees that are inspired, in part, by release from competition with non-crop

vegetation (e.g. B.C. Ministry of Forests, 2000; Knopp and Stout, 2014), however these standards are not always informed by maximum heights of both competing vegetation and ungulate browsing. Furthermore, no such standards exist for many areas and/or stakeholders. We suggest that surveys intended to assess regeneration success consider only saplings that are “free to grow” from both shrub competition and ungulate browsing.

Given that current forest conditions over large extents of temperate forest in Eastern North America are characterized by low diversity tree sapling recruit classes dominated by shade-tolerant, browsing-insensitive species of low economic value (i.e. species that would fit in our *Broad* category), it is clear that the current management combination of low-intensity selection silviculture and the maintenance of high deer populations is not working in many regions. (Kern et al., 2017, Webster et al., 2018, Vickers et al., 2019, Elenitsky et al., 2020). Few examples exist of deer-forest co-management aimed at maintaining both healthy deer populations and diverse well-stocked tree regeneration (Pennsylvania DCNR, 2013). If current management paradigms persist, forest diversity, resilience, and sustainable management will erode (Millington et al., 2011, Jactel et al., 2017, Webster et al., 2018, Sabo et al., 2019). For forest management, implementing a range of silvicultural systems that collectively vary canopy harvest disturbance severity, particularly systems that increase the representation of more severe canopy disturbances than are currently used, will be important (Raymond et al., 2009, Kern et al., 2017, Webster et al., 2018, Walters et al., 2020). Our data suggests that openings must be > 0.3 ha in size with > 60% gap light to promote sapling recruitment of *High Light* species in areas of moderate to intense deer browsing pressure (Fig. 4). Silvicultural systems potentially matching this harvest intensity requirement include patch-cut, shelterwood, and seed tree systems, however these systems need to be tested and refined for many temperate forests given limited historical trials and application (Walters et al., 2020). An important caveat is that our recommendations may be applicable in the context of current high deer populations, but might not be effective at even higher deer populations. If more intense harvest regimes are adopted broadly by managers, increased browse availability could further increase deer densities (Leopold, 1950) and negate the potential benefits of changed forest management for sapling recruitment.

Decreasing deer populations, where there is public will, should increase sapling recruitment for most species, and will be critical for slow-growing, browsing-sensitive species of the *Nowhere* group. Given height growth rate patterns for planted seedlings and dense, diverse regeneration < 1 m tall (though not > 1 m tall) in stands with high deer densities, we suggest that reducing regional deer densities periodically for ~10 years combined with more severe canopy disturbances than single tree selection creates may be sufficient for sapling recruitment of most species. Reducing deer could be combined with planting seedlings in cases where advance regeneration is insufficient. Notably, some species that are particularly sensitive to deer browsing and have very low height growth rate potential (e.g. *T. occidentalis*, *T. canadensis*) may be particularly difficult to regenerate without > 20 years of deep reductions in deer populations.

Our data clearly indicate that faster height growth rates increase recruitment success in the face of shrub competition. Given that height hierarchies for tree seedlings and competing shrub layers depend on their respective height growth rates and timing of establishment, managers should rapidly establish larger and/or faster-growing tree regeneration immediately following overstory harvest, whether by planting, seeding, or silvicultural treatments aimed at improving conditions for natural regeneration (e.g. scarification, Prevost et al., 2010, Willis et al., 2015, timing harvests with mast seed years). This practice should especially benefit species in the *High Light* group. In addition, the legacy of over 60 years of high deer populations and selection silviculture in many areas is a dense, competitively-dominant, low-diversity sapling layer of *Broad* group species. Density of this stratum may need

to be reduced with herbicides or other means in order to recruit a more species-diverse sapling layer.

Lastly, the changes in silviculture and/or deer management necessary to increase the diversity and representation of currently under-represented species in northern temperate forests via natural regeneration will also be important for assisted (and passive) migration and diversity enrichment planting efforts (Nagel et al., 2017). Our results for planted seedlings in an area of just moderately high regional deer densities (Walters et al., 2016) suggest that if these species were planted as part of a climate adaptation/diversity enrichment program, 40% would have virtually no chance of recruiting saplings (*Nowhere* group). That leaves 60% of the species as candidates for planting: 40% (*Broad*) that could be planted over a larger range of harvest openings and another 20% if management changed to include larger harvest gaps (*High Light*). However, some of these planting candidates would still likely experience high pre-recruitment mortality from deer browsing pressure and shrub competition. Given these circumstances and the inherently high cost of planting, we suggest that diversity enrichment and/or climate adaptation plantings should focus on low-density plantings, where the likelihood of recruiting saplings through deer browsing and shrub competition bottlenecks is enhanced by using large planting stock, protection from deer browsing (e.g. grow tubes, fencing), or other means. We argue that over timeframes greater than tree lifetimes and/or stand rotations, the value of recruiting site-novel species at low densities is very high for ecosystem resilience.

#### Author declaration

Walters was primary in conceptualization, sole in terms of analysis, securing funding and writing of the original draft. Willis and Farinosi also contributed to conceptualization, investigation, writing:reviewing/editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118134>.

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