Forests for Dinner: Exploring a Model of How Deer Affect Advance Regeneration at Stand and Landscape Scales

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Abstract: *White-tailed deer herbivory is widely perceived by forestry professionals to be the leading cause of regeneration failure in managed uneven-aged forests in the Eastern United States. However, few studies have examined the chain of processes that link deer density, landscape structure, herbivory, and forest composition and structure. In this paper we identify and quantify some of these linkages in northern hardwood stands within a ~400,000 acre study area in Michigan's western Upper Peninsula. In this region we found that winter deer density in a focal northern hardwood stand could be predicted by distance to winter thermal cover (i.e. conifer forest). However, observed browse damage to tree seedlings in a stand was not a simple function of winter deer density whether measured overall or subset by tree species. We tested seedling stem density in three height categories representing browse-susceptible (0.5 to 1.5m tall), browse-marginal (1.5 to 2.5m tall), and browse-escaped (2.5 to 5.5 m tall). Overall stem density remained constant in the browse-susceptible size class, and decreased with increasing observed browse damage in the taller height classes. Analyzed by species, stem density in each of these height categories generally decreased for Acer saccharum, a preferred-browse species, and generally increased for Ostrya virginiana, a non-preferred species, with increasing average browse damage at the stand level, and also with increasing local deer density. In summary high deer browse pressure decreases the recruitment of tree seedlings to taller height classes and changes the composition of the seedling community to less preferred browse species*.

Introduction

White-tailed deer herbivory is widely perceived by forestry professionals to be the leading cause of regeneration failure in managing uneven-aged forests in the Eastern United States. There are scores of studies that quantify the effect of deer presence and absence on forest vertical structure. These studies mainly document two effects of deer herbivory: regeneration failure (Bowles and Campbell 1993;Kittredge and Ashton 1995;Anderson and Loucks 1979;Anderson and Katz 1993;Strole and Anderson 1992), and shifts in the understory species composition of local vegetation communities (Alverson et al. 1988;Waller and Alverson 1997;Stromayer and Warren 1997;Augustine et al. 1998;Tilghman 1989). Mainly these studies have either used exclosures to contrast 'ambient' deer density with zero deer density, or have contrasted forest characteristics in high-deer-density vs. low-deer-density landscapes. Few studies have quantified the sensitivity of forest vegetation to a continuous range of deer densities (but see (Tilghman 1989), and no study of which we are aware has examined the processes that link deer density, landscape structure, herbivory, and vegetation community composition and structure. This information is important because real forested landscapes are characterized by broad ranges of deer densities that are highly variable spatially, and deer density impacts on forest regeneration are likely best described as a continuous function. In other words, forest managers are not confronted with decisions based on the homogeneous presence of high deer densities or absence of deer. Instead they confronted with questions like 1) how many deer is too many to regenerate desirable species at sufficient densities? and 2) how does proximity of a managed stand to winter deer yards influence deer density and thus browsing pressure on regeneration.

In this paper we identify and quantify some of the linkages among deer, landscapes, and vegetation. Quantifying these linkages is critical to understanding whether, why, and how deer affect plant communities including advance reproduction in uneven-aged forest silvicultural systems. By extension, a quantitative understanding of these mechanisms may shed light on how best to work with and limit negative deer impacts on vegetation in an environment of high deer density.

Hypotheses

We propose a conceptual model for studying deer-forest interactions, and specifically the effect of deer herbivory in uneven-aged northern hardwood forests (

Figure 1). The conceptual model identifies the specific core factors that we hypothesize to drive deer-landscape-vegetation interactions in these forests. We hypothesize that:

1. Local deer density within a given northern hardwood forest stand is driven by the amount of winter thermal cover nearby;
2. Browse damage to seedlings and saplings is correlated with local deer density;
3. Deer browse intensity varies with tree species;
4. Seedling densities in critical height classes within a stand are negatively correlated with deer density and deer browse intensity;
5. The correlation between stem density in critical height classes and deer density varies with species.

Methods

We collected field data on vegetation community structure and composition in northern hardwood forest between 2001 and 2003. White-tailed deer fecal pellet density was surveyed on transects surrounding the vegetation plots, and was used as an index of deer use of local landscapes between 2002 and 2004. We used landcover map developed for the state of Michigan from classified satellite imagery (Space Imaging Solutions 2001) as a measure of landscape composition. Data were analyzed using least squares regression available in the R open source statistical package (R Development Core Team 2004). Detailed methods are as follows.

Study Area and Study Sites

The study region comprises ~400,000 ha in the Upper Peninsula (UP) of Michigan (Figure 2). The region was chosen to focus on a primarily forested region with a minimum of intensive human land uses such as agriculture, urban, suburban, or rural settlements see (Laurent et al. In Press). The primary land use in the study area is forest management for timber products.

A total of 145 study plots located in northern hardwood forest were surveyed for vegetation characteristics and fecal pellet group density in 2002, 2003, or 2004 (see Laurent et al. In press). In general, we used a stratified random procedure to select study sites as follows. In a GIS environment (ArcView 3.2) we randomly selected landscape units (LU) of either USGS quarter-quarter quads or General Land Office survey sections (2002 and 2003). Within each randomly chosen LU, plots of 30m radius chosen for vegetation sampling based on ownership, land cover, and proximity to other sampled plots. Survey plots encompassed a 30-m radius area to roughly match the spatial resolution of a single pixel of Landsat 7 ETM+ imagery (used to classify land cover) sensed over plot centers. The specific plot selection was made in the field using the criterion that a hypothetical 30-m x 30-m square could be placed anywhere within the plot and perceived by the field crews as having the same vegetation structure and composition as a similar square placed anywhere else within the plot.

Deer Density Data

Fecal pellet counts provided a convenient and spatially explicit index of deer density across a landscape (Litvaitis et al. 1996). White-tailed deer fecal pellet group deposition rates are affected by time of year, food availability, weather, stress, and in general the health of a deer herd (Litvaitis et al. 1996). Despite these many complicating factors, a simple approach to estimating deposition rates may be sufficient for many purposes (Hill 2001). However, the index is not comparable to a true estimate of population sizes across deer range, which requires more detailed demographic data.

There are several factors that need to be measured or assumed in order to use fecal pellet counts as a spatially precise estimate of deer density. These include: 1) the rate of production of pellet groups (pellet groups/deer/day), 2) the period of time over which they are deposited; and 3) the degree to which deer deposit fecal pellet groups randomly with respect to their daily movements. For example,(McCain 1948) estimated that mean deer pellet deposition is 13.4 pellet groups/day in Michigan, while (Fuller 1991) used 33 pellet groups/day in Minnesota. In this paper we use the Michigan figure of 13.4 pellet groups/day because it allows comparison with State of Michigan deer population calculations based on historical Michigan Department of Natural Resources (MDNR) pellet group surveys.

At each of 145 study plots with deciduous or mixed forest types, we positioned and surveyed ten transects arranged in a “bow tie” configuration established within a 155m radius of the plot center (7ha, Figure 1c).. Each of the ten transects measured 50x4m (0.02ha). Within each fecal pellet group survey transect, we sampled pellet group density using a modification of the MDNR annual deer pellet sampling methodology that has been performed since 1959 (Hill 2001). We performed all surveys between April 30th and May 20th in three survey years (2002, 2003, and 2004), to represent winter deer density for the time period beginning with leaf-off and ending with counting date. Deer pellet density estimates from all ten transects were averaged to arrive at a deer density index for the landscape surrounding each vegetation plot.

Vegetation Data

We collected data on species, stem density, and stem height for understory woody vegetation >0.25m and <1.5m tall for each vegetation plot. Data were collected on a 3 by 3 grid of sample points located within a 30m radius of each plot center. N-tree distance sampling was used for tree density (Lessard et al. 1994). From each survey point within a plot, we measured the distance to the nearest 5 trees. Species, height, diameter at 10cm above the ground, and browse category (Table 1) were recorded for each of the 5 closest trees. Density estimates were generated following Lessard et al. (1994). Because many of the species encountered were present at a small subsample of sites, we used only the two most common species in these analyses: *Acer saccharum* (sugar maple) and *Ostrya virginiana* (ironwood).

Landscape Description

The land cover map was used to describe areas surrounding sampled plots. In ArcView 3.2, the distance from each vegetation plot center to the nearest conifer land cover was measured. This distance to conifer was used as the descriptor of the landscape context of each stand.

Deer Density vs. Distance Analyses

The relationship between local winter deer density and distance to the nearest conifer stand was analyzed in two different ways: 1) average deer density as a function of distance from the nearest conifer stand; and 2) maximum deer density in each of 16 distance categories (0-50m, 50-100m, …, 750-800m) as a function of distance from conifer. The first analysis assumes that distance to conifer is the main landscape factor; if this is the case, low deer density and high deer density areas should both be predicted equally well. The second analysis assumes that distance to conifer is a limiting factor only, and that deer require conifer in a mix with other resources. In this case, distance to conifer would be correlated with the upper limit of deer density at a site, but not necessarily with the lower limit of deer density.

Results and Discussion

1. Local deer density on a landscape was driven by the distance to winter thermal cover.

An analysis of observed deer density as a function of distance to coniferous forest showed that both average deer density (β=-0.004, R^2=0.03, p<0.001) and maximum deer density (β=-0.013, R^2=0.19, p=0.015) were negatively correlated with distance to conifer (Figure 3). While only 2.5% of the variation in average deer density was explained by distance to confer, 18% of the variation in maximum observed deer density in 50m distance categories was explained by distance to conifer cover. Thus, the maximum number of deer was highly sensitive to distance to conifer, but, at short distances to conifer deer numbers vary broadly, presumably because they are reacting to factors other than proximity to conifer at those distances.

2. Browse damage to seedlings and saplings was correlated with local deer density.

Browse damage of saplings <1.5m in height of all woody species showed a saturating response to deer density (Figure 4) because it increased rapidly with increasing deer density at low deer densities (0-5 deer/km^2), but increased more slowly (approaching a maximum of ~2.5) at deer densities >20/km^2 (Figure 4). The relationship was significant (p=0.018), but explained only 3.8% of the overall variation in browse index by using site-level winter deer density alone (Figure 4). Part of the difficulty with this analysis was that winter deer density is measured for a time period including only the previous winter, while the browse damage measurement effectively integrates any browse damage that has occurred over the life of the seedling being measured, which may be several years or even decades in the case of some species, depending on the stand.

3. Deer browse intensity varied with local deer density, but NOT with tree species.

Examining each species separately revealed that both *A. saccharum* (a preferred-browse species) and *O. virginiana* (a non-preferred browse species) exhibit a similar pattern of browse damage with increasing winter deer density (Figure 5). This is not intuitive, and indicates how little we really know about how deer affect different species on the ground. We had hypothesized that browse-preferred species such as *A. saccharum* would be more intensely browsed as deer density increased, while non-preferred browse species would not be as intensely browsed. However, the data indicate that both species respond similarly to increasing local winter deer density. This is a very interesting result, and requires further study. It suggests that browse damage occurs to both of these species equally, and is not limited mainly to purportedly preferred-browse species.

4. Seedling densities in critical height classes within a stand were negatively correlated with deer density.

Seedling density in the browse-susceptible height class (0.5 to 1.5m tall) was not affected by deer browse pressure (Figure 6a), but responded negatively to local winter deer density (Figure 6b). Seedling density decreased with increasing browse pressure in height classes recently escaped from deer browse pressure (1.5 to 2.5m tall, Figure 6c). However, stem density in this recent escape height class increased with local deer density from 6 to approximately 18 deer/km^2. At deer densities above 18/km^2, stem density in this 1.5 to 2.5m height class was virtually zero (Figure 6d). In the tallest sub-canopy height class (2.5 to 5.5m tall), stem density generally decreased with browse category (Figure 6e), and also decreased with deer density (

Figure 6f) except for the 18 deer/km^2 level. This result indicates that 18 deer/km^2 may be a threshold deer density, beyond which seedlings of any species are unable to grow quickly enough to escape deer browse pressure. Interestingly, this is the same threshold deer density observed by Tilghman (1989).

5.1 The correlation between deer density and stem density in critical height classes varied with species.

We compared stem density of two key overstory species to both observed browse damage to existing understory seedlings, and to observed local deer density. Stem density of *Acer saccharum* in the browse-susceptible height class decreased by more than half (from 5000 to 1800 stems/ha) as observed deer browse damage increased (Figure 7a). In the same stands, stem density of *Ostrya virginiana* doubled (from 900 to 1800 stems/ha) over that same browse damage gradient (Figure 7b). In the recently escaped height class, *A. saccharum* showed no change in stem density with increasing browse pressure (Figure 7c), while *O. virginiana* increased 300% as average browse damage increased from <10% to >90% of available twigs (Figure 7d). In the tallest height classes, *A. saccharum* again showed little decrease in stem density per ha as browse damage increased (Figure 7e), while *O. virginiana* increased 600% as browse damage increased from <10% to >90% (Figure 7f).

5.2 The correlation between browse damage and stem density in critical height classes varied with seedling species.

Comparison with observed local deer density returned less clear-cut results. *A. saccharum* density in browse-susceptible height class decreased from 0 to 18 deer/km^2, but increased greatly in the highest deer density stands (Figure 8a). *O. virginiana* showed no change over that deer density gradient (Figure 8b). Recently-escaped *A. saccharum* seedlings 1.5 to 2.5m tall decreased from an average of 125 stems/ha to less than 50 stems/ha (Figure 8c). *O. virginiana* stem density in the same height class decreased from 160 to 40 stems/ha from 0 to 18 deer/km^2, but increased to 100 stems/ha in the highest deer density class (24 deer/km^2). However, the highest deer density class was represented by only two sites, so may not have been a reliable estimate of actual behavior of the deer-forest system.

In summary, browse intensity was more highly correlated with seedling densities in these height classes than is local deer density. This was likely because the browse damage measurement takes into account damage from previous seasons as well as the year in which it was measured, but local deer density is specific only to the year in which it was measured. Tree seedlings exist in the understory for many years, so browse damage was probably a better measure of long-term deer effects on tree regeneration than was the local density of deer in any given year.

Summary and Conclusions

Four of our five hypotheses were corroborated by our data: 1) local winter deer density is greater in stands near to winter thermal cover; 2) browse damage to seedlings is greater with higher deer density; 4) Seedling density decreases with browse category and deer density in all height classes considered; and 5) the relationship of stem density to deer density and to deer browse varies with tree species observed. Contrary to the third hypothesis, the correlation between browse damage and local winter deer density did not appear to vary by tree species. However, it appeared that deer do affect vertical structure (i.e., stem density in different height classes) and species composition of the vertical structure regardless of whether deer browsed different species at different intensities.

Based on these results, it appears likely that deciduous forest stands near to conifer stands may be characterized by a distinctive vertical structure such as a higher density of seedlings in the height class 0.5 to 1.5m tall, and a lower density of saplings in taller height classes (1.5 to 5.5m tall). It is also possible that a change in species composition will be caused by high deer density, resulting in stands with more *O. virginiana* and less *A. saccharum* in the understory, and eventually in the overstory, in landscapes where deer density is high. Nevertheless, not one of these relationships explains a large percentage of the variation in stem density.

There are several possible reasons for this which require further study. Stand productivity (e.g., site index or Habitat Type) was not considered in this study, and may have an important bearing on the composition, density and growth rates of regenerating trees. Likewise, stand history was not accounted for in this study, other than to limit the study to stands between 20 and 31m^2/ha (90 and 140ft^2/acre) basal area. Higher density of seedlings and saplings is expected for some successional stages than for others. A third important consideration is how these relationships vary across the study region; for example, is distance to conifer more important in areas where there is less conifer (e.g., western Marquette county) and less important where conifer is very common on the local landscape (e.g., northern Menominee county)? Is conifer more important in the snow belt than in the southern part of the landscape?

Finally, deer density and deer browse data used here were gathered over a very short time, and represent a snapshot of the state of the forest between 2001 and 2004. Seedlings of the tree species we studied often occupy the forest floor for decades, and deer populations fluctuate annually and across decades. Even as we try to understand and document the present relationship between deer and tree seedling dynamics, we should acknowledge that the relationship itself is the summation of forest management, wildlife management, and natural disturbance regimes superimposed on a landscape over a century or more. Therefore the relationships between wildlife and forest management is a response to several dynamic forces, including forest and wildlife management strategies themselves. The interactions between wildlife and forest vegetation are complex, and may not always be intuitive. Thus careful observation and tracking of the results of management activities must be conducted, and the assumptions behind management decisions need to be reevaluated frequently to ensure that both forestry and wildlife goals can be met.

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Tables and Figures

Table 1. Browse category explanation. Browse category is measured on individual seedlings (45 seedlings/plot). It represents the proportion of twigs and branches on each seedling that show evidence of deer browse divided by the total number of twigs/branches on the seedling.

Browse Category	%Browse
0	0 to 1
1	1 to 10
2	10 to 50
3	50 to 90
4	90 to 99
5	100

Table 2. Regression results for models of local deer density as a function of distance to conifer. The model of average deer density includes all sites. The model of maximum deer density includes the site within each 50m distance category in which the maximum deer density was observed.

y	Beta	R2	p-value
Distance (average deer density)	-0.004	0.026	<0.001
Distance Category (maximum deer density)	-0.013	0.188	0.015

Table 3. Regression of Michaelis-Menton (saturation) function results to predict browse category. Vmax=1, k=1.

Coefficients:	Estimate	Std.Error	t value	Pr(>|t|)	
(Intercept)	1.5740	0.2169	7.258	4.37e-11	***
pred	1.0058	0.4211	2.389	0.0185	*

Signif. codes: 0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1
Residual standard error: 0.725 on 119 degrees of freedom
Multiple R-Squared: 0.04575,   Adjusted R-squared: 0.03773
F-statistic: 5.705 on 1 and 119 DF, p-value: 0.01849

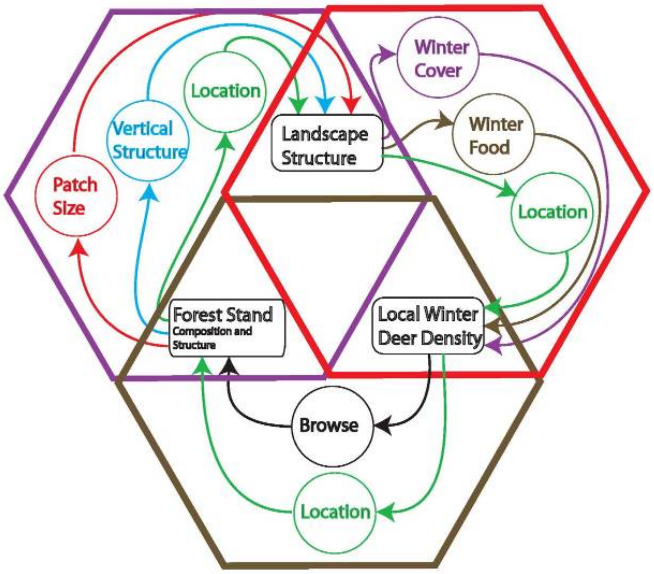


***Figure 1**. Conceptual model of pathways among landscape characteristics, winter deer density, and forest stand structure and composition.*

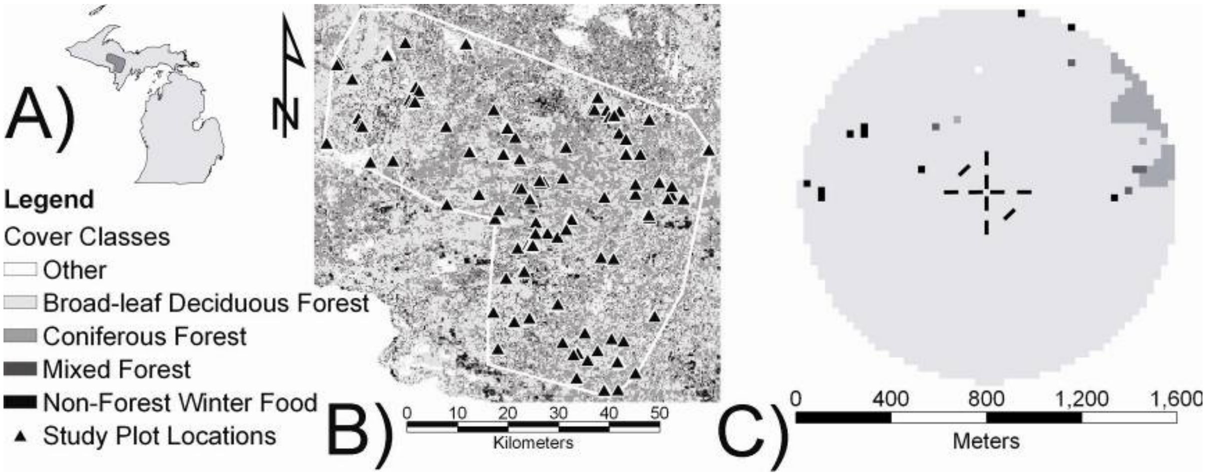


***Figure 2**. Study area. A) Location of study area in Upper Peninsula of Michigan, USA. B) Locations of study sites within study area. C) Example 800m radius landscape with deer pellet transect locations. Vegetation plot is located in the center of the deer pellet transect.*

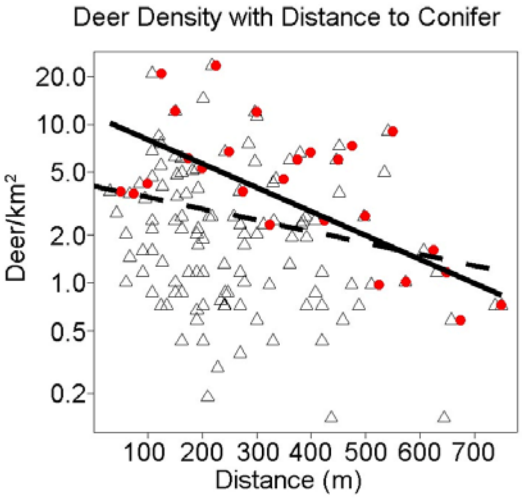


***Figure 3**. Local winter deer density response to distance from conifer land cover. Open triangles and dashed line indicate relationship of deer density to distance for all sites. Filled circles and solid line indicate highest deer density observed within each of sixteen 50m distance categories. Distance is treated as an ordinal variable in this analysis.*

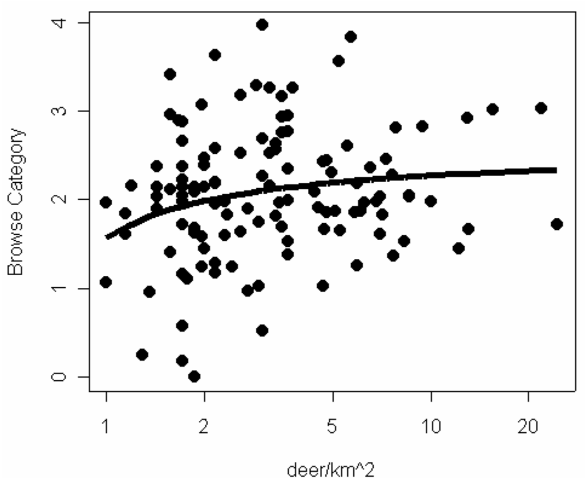
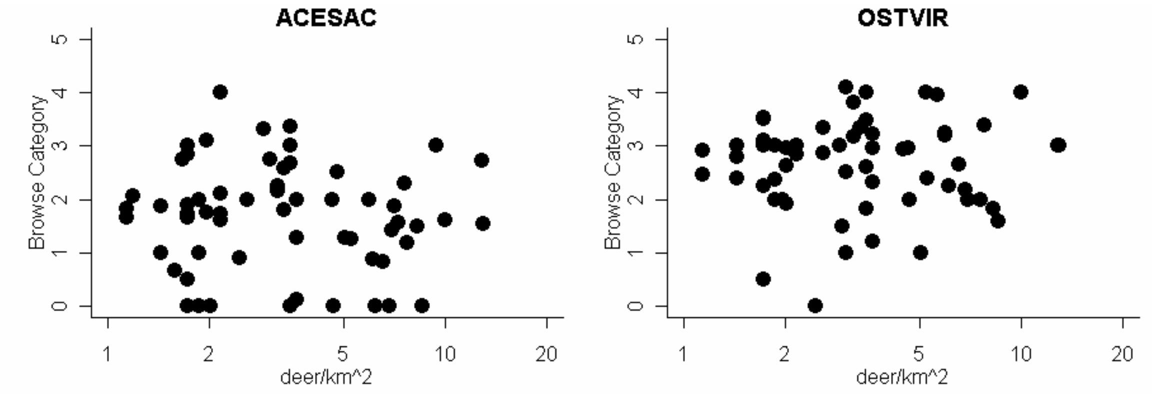


***Figure 4**. Browse index vs. winter deer density follows a Michaelis-Menton model with maximum expected browse index = 2.5 (i.e., Vmax + regression intercept), and the critical density (k) = 1 deer/km^2. Browse index of 2.5 corresponds to 10-50% of available twigs being browsed.*



A)

B)

***Figure 5**. Biplots of browse damage occurring to seedlings <1.5m tall of Acer saccharum and Ostrya virginiana across a range of local winter deer densities. Local deer density alone is not a good predictor of local browse damage.*

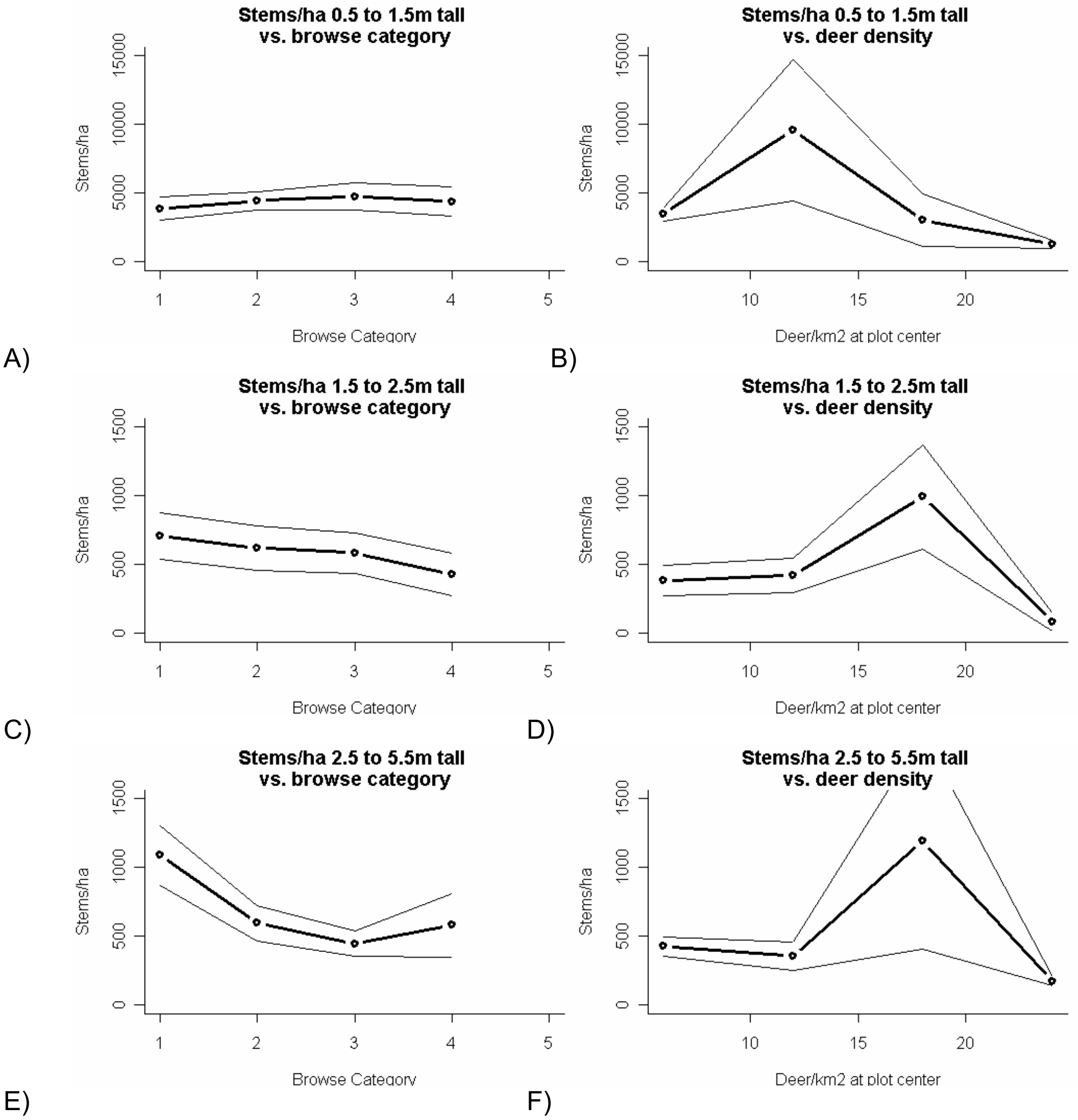
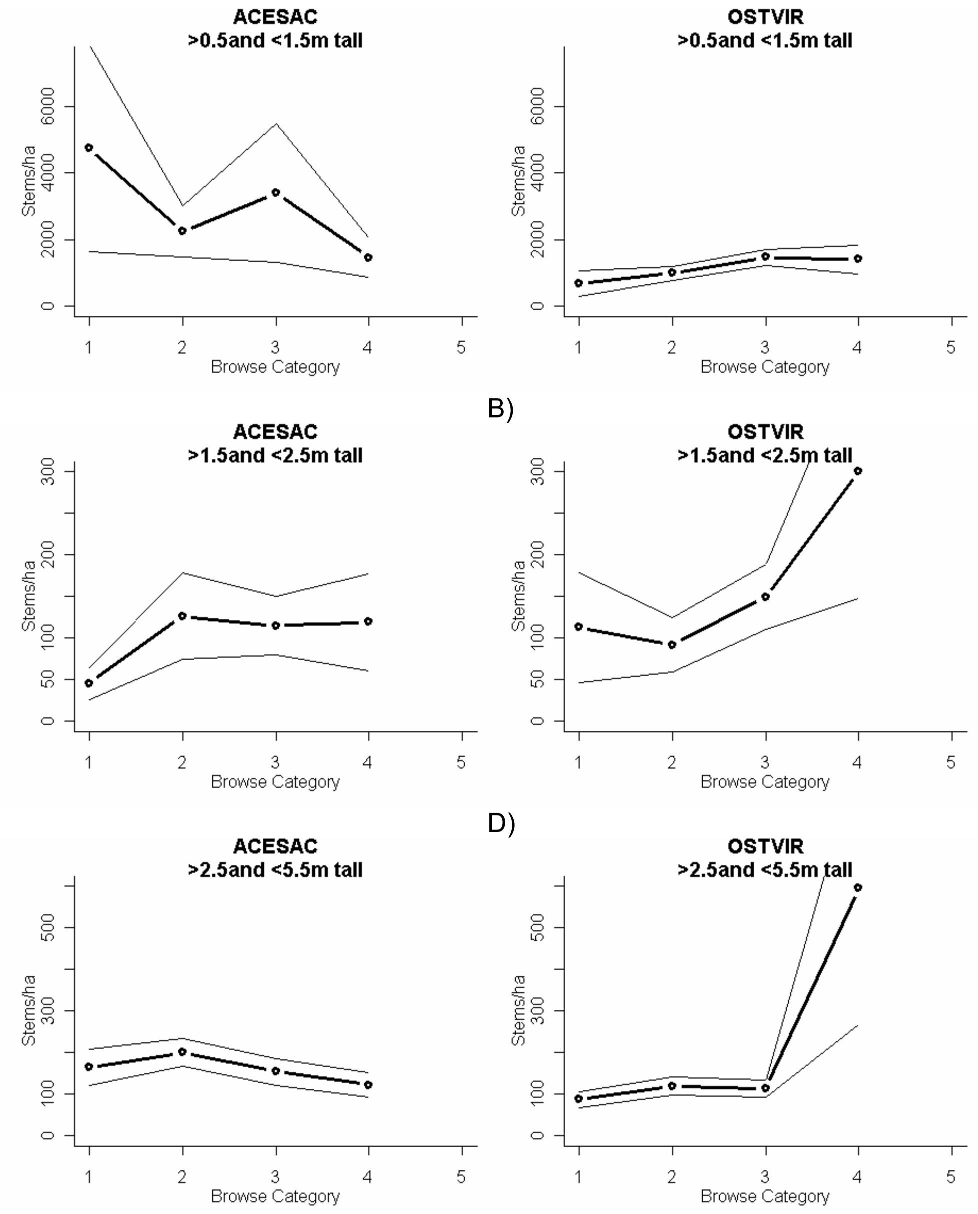
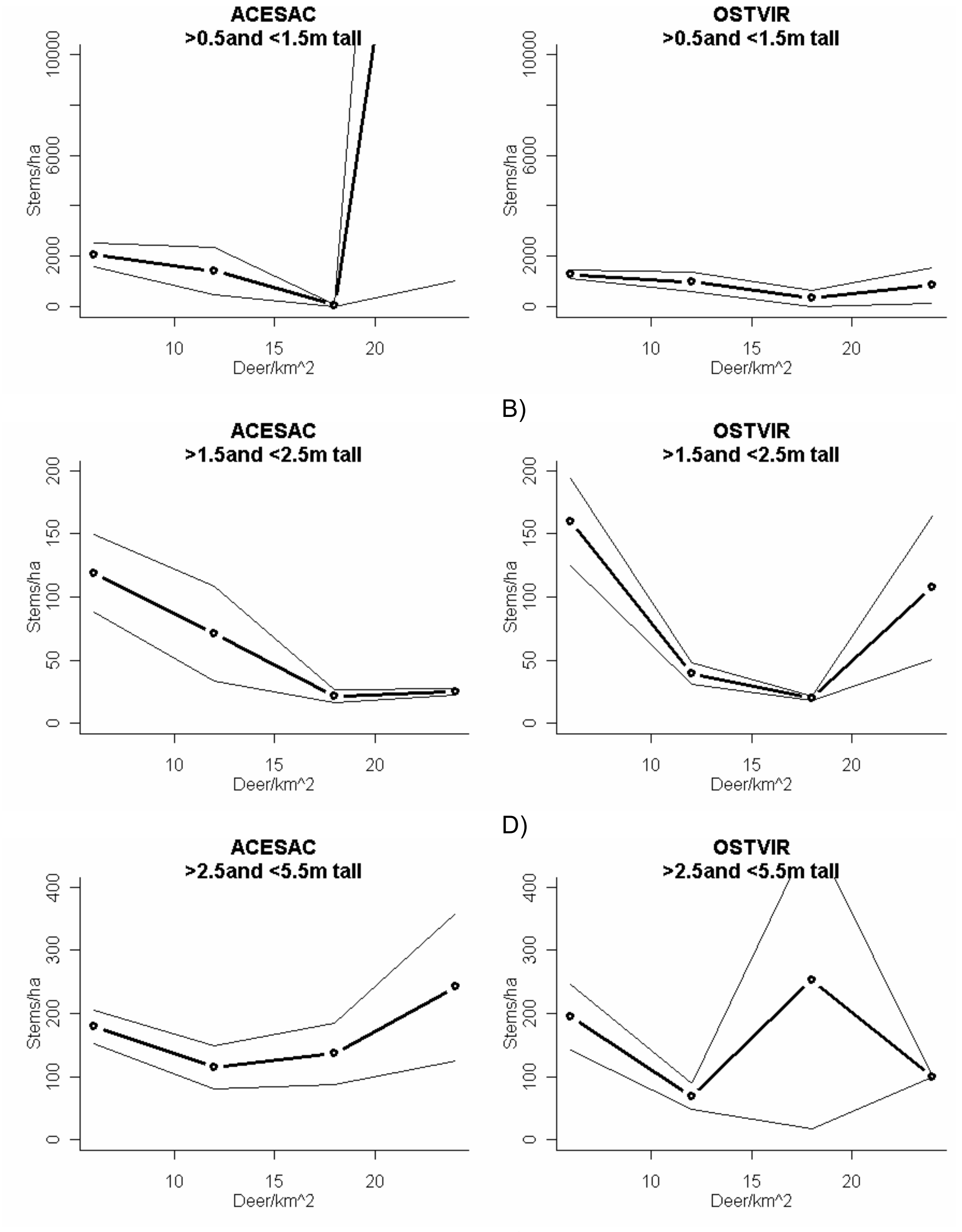


Figure 6. *Seedling density in three height classes vs average browse intensity category across all seedlings >0.5 and <1.5m tall. Sample size n = 25, 76, 77, and 21 sites for browse categories 1, 2, 3, and 4, respectively. For deer density data, n = 85,16, 3, and 3 sites, respectively, for 0, 12, 18, and 24 deer/km^2, respectively. Thick lines are the average stem density per site within each browse category or deer density category; thin lines are one standard error of the mean above and below the mean value. Browse damage measurements account for seedling damage due to deer that occurred several years prior to the measurement. We assume that the browse damage assessment, as an indicator of past as well as present browse pressure, indicates conditions that were prevalent during the time the taller height class tree seedlings (i.e., those >1.5m tall) were within browse range (i.e., 0.5-1.5 m tall.) In contrast, deer density represents only the previous year's condition (though it may indicate a long-term local trend in deer density).*



A) B) C) D) E) F)

Figure 7. *Stem density for three height classes of Acer saccharum and Ostrya virginiana in relation to site-average browse category. Sample size n=5, 48, 57, and 16 for browse categories 1, 2, 3, and 4, respectively. Thick solid lines are the average stem density per site within each browse category or deer density category; thin lines are one standard error of the mean above and below the mean value. See Figure 6 legend for details regarding browse category assumptions.*



A) B) C) D) E) F)

***Figure 8**. Stem density of three height classes of seedlings and saplings in relation to local winter deer density. Sample size n=103, 12, 2, and 2 for both species in deer density categories 0-6, 6-12, 12-18, and 18-24, respectively. Thick solid lines are the average stem density per site within each browse category or deer density category; thin lines are one standard error of the mean above and below the mean value.*

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