Density and diversity of tree species in treefall canopy gaps with respect to shade tolerance and browse tolerance levels

BIOS 35502: Practicum in Environmental Field Biology

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Abstract

Canopy gaps and browsing are two important factors that determine the tree species composition in a forest. The gap hypothesis outlines the importance of canopy gaps in maintaining the regeneration of various tree species, especially pioneer trees that need high levels of light to survive. The interaction between low shade tolerant pioneer species and canopy gaps is well documented, but the same cannot be said about highly shade tolerant tree species. Whether or not the gap hypothesis can be extended to these shade tolerant species is unclear. Additionally, increases in the number of browsers in the past few decades may be negating the effects that canopy gaps have on forest composition. Heavy browsing has been shown to reduce the effects that canopy gaps have on tree regeneration. This study determines and compares the tree composition in gaps and in closed canopy areas in order to assess differences between the two in terms of the browse and shade tolerance of the plants represented. The lack of significant increases in pioneer species in gaps and the high levels of highly browse tolerant species both within and without gaps suggests that over browsing is selecting for tree species that can withstand heavy browse and do not rely on canopy gaps to regenerate.

Introduction

The gap hypothesis makes predictions about the relationship between treefall gaps and the maintenance of forest diversity (Schnitzer et al 2008). It states that that treefall gaps make light available to species that are unable to grow or thrive without it and that within gaps there is a heterogeneous resource gradient allowing species with different resource requirements to coexist in an otherwise similar environment. Additionally, the gap hypothesis is related to the intermediate disturbance hypothesis which asserts that disturbances that are intermediate in size increase diversity in an ecosystem (Schnitzer et al 2008). Whether or not treefall gaps can be considered an intermediate disturbance and therefore increase forest diversity is an important distinction to consider. There is a large amount of evidence supporting the maintenance of shade intolerant pioneer species diversity by canopy gaps (Clark et al 1993, Dalling et al 1998, Whitmore 1989). However, there is little evidence to support the maintenance of shade tolerant species diversity. In fact, the little evidence that there is actually does not support this assertion (Schnitzer and Carson 2001). Without proper evidence to document shade tolerant diversity maintenance by canopy gaps, it remains unclear whether the intermediate disturbance hypothesis can be extended to canopy gaps. This study examines the tree species present in gap areas and non-gap areas in order to determine if shade tolerant species diversity and abundance is increased in canopy gaps.

Browsing, by deer and other animals, greatly impacts tree species diversity (Nuttle et al. 2013). Deer populations increased by as much as 600% in Wisconsin from 1950 to 2006, resulting in over browsing (Cutright and Kearns 2010). Logically, an increase of browsing would result in the selection and propagation of tree species that are more browse tolerant. Effects of this increase in browsing on the diversity and composition of forests have been documented in many regions across the eastern United States. The high white-tailed deer density in the northern great lakes region have caused hemlock (*Tsuga canadensis*) populations to decline, giving way to the more browse resistant sugar maple (*Acer saccharum*) (Frielich and Lorimer 1985). Recruitment failure of hemlock and white cedar (*Thuja occidentalis*) has also been partially attributed to deer browsing increases (Rooney 2001). At the University of Notre Dame Environmental Research Center (UNDERC) in northern Wisconsin/Michigan where this study took place, there have been significant increases in the deer population (Wisconsin DNR 2016). Parts of the UNDERC forest area is made up of maple, and therefore over browsing may similarly be affecting forest diversity. The relatively recent explosion in the deer population along with increases in other browser numbers in the last few decades has likely skewed the importance of tree characteristics in favor of browse tolerance, perhaps reducing the significance of shade tolerance as an advantageous trait.

My study examined tree species composition in terms of both shade and browse tolerance in gap and closed canopy areas. By comparing sampled gap areas with adjacent non-gap areas, I was able to observe the effects that canopy gaps have on tree species composition. This allowed me to address the gap hypothesis in terms of the maintenance of species diversity, focusing on the under documented aspect concerning shade tolerant species. This study considers the density and relative abundance of trees based on their shade and browse tolerance levels (low, intermediate or high for each) and how they differ between gap and closed canopy. Additionally, the difference between how trees are browsed in gaps versus in the surrounding forest is assessed. The expectation is that gap seedlings will be browsed at a higher rate as they have access to more resources and therefore will be more nutritious.

I tested several hypotheses as follows: (1) Pressure from deer browsing will result in high-browse tolerant species being more abundant than intermediate- and low-browse tolerant species in both gaps and non-gaps; (2) browsing will be more prevalent in gaps than in the closed canopy and therefore (3) high-browse tolerant species will be relatively more abundant in gaps than in non-gaps; and (4) high-shade tolerant species will have a higher absolute abundance in gaps than in non-gaps due to increased resources, thereby extending the gap hypothesis to shade-tolerant species.

Methods

This study was conducted at the University of Notre Dame Environmental Research Center (UNDERC). For the purpose of this study, a canopy gap is considered a break in the canopy larger than 100 m^2 due to one or more fallen or dead trees (Schnitzer et al 2008). After 26 canopy gaps were located in various places on the UNDERC property (Figure 1) and their size was measured, the gaps were sampled. For comparison in the data analysis, control non-gap areas 15 m from each gap were sampled with the same sampling procedure as the gap areas. The gaps and non-gap controls were divided into quadrants, each quadrant with a 1x5 m rectangle radiating out from the center of the gap assigned in randomly chosen compass directions (Schnitzer and Carson 2001). This gave an area of 20 m^2 sampled for each site. The trees within the transects that were >1 m in height were identified and tallied. Counts from each of the four transects were combined for each gap to calculate the density and diversity of trees in each gap.

Each of the tree species found in sample areas were assigned a ranking of high, medium or low for both shade tolerance and browse tolerance. The 15 tree species that were found in the sampled areas fall into one of 9 categories labelled according to their browse and shade tolerance levels respectively, as seen in Figure 1. The tolerance groups will be referred to in this manner throughout the rest of the paper, with browse-shade levels. Note that none of the tree species observed fell into the High-Low or Low-High categories. Shade tolerance is established for most tree species, so rankings are in the literature for the various tree species at UNDERC (USDA Natural Resources Conservation Service 2016). The browse tolerance is determined by the ability of the species to survive after sustaining damages from browsers. I used characteristic data from multiple government databases and compilations (Burns and Honkala 1990, Wisconsin DNR 2015, USDA Natural Resources Conservation Service 2016) and gathered data from other scientists and studies (Rooney 2016; Carson 2016).

To assess difference between gaps and canopy plots, I first subtracted the relative abundance, density, and richness of canopy plots from their paired gap plot. This means that values above zero indicated an increase in the measure in the gaps, values below zero indicated a decrease in the gaps. Then I tested whether these differences in RA, D, and R varied significantly among tree tolerance groups using 2-way ANOVAs. I also performed multiple comparisons with a Tukey HSD test for all the ANOVA with significant differences to provide information on whether specific tolerance groups are statistically different from one another.

Additionally, I haphazardly selected 20 maple saplings in both the gap and non-gap areas and examined them to determine if they had been browsed by deer. The saplings were at least 50 cm in height but no taller than 2 m. Some gaps that did not have enough sugar maple saplings either in the gap or in the surrounding area and were not included in the data analysis. To determine if there was a significant difference in the level of browse on sugar maples between gaps and closed canopy areas, I ran a paired t-test comparing the gap sites and the non-gap sites.

Results

Over the course of this study, 26 gaps and 26 corresponding closed canopy areas were sampled. The largest gap sampled was 624.64 m^2, the smallest 120 m^2 and the average gap size was 273.32 m^2. A total of 1005 trees were counted and identified and 15 different tree species were found.

In order to perform ANOVAs for the relative abundance, species richness and density of tree species across the shade and browse tolerance categories the similarity in the variances between groups was assessed with Fligner Tests. All of the groups for shade and browse tolerance (high, intermediate and low for each) in each data set were found not to be significantly different, so ANOVAs were used (Table 2).

Patterns in Density

The density generally increased in the gaps, on average there were 14.35 more trees in the gaps than in the closed canopy. The density of tree species significantly differed by shade tolerance levels (Figure 3) and there was a significant interaction between browse and shade tolerance (shade tolerance, df=2, F=8.99, p=0.000175; interaction df=4, F=4.3137, p=0.0022117, Table 3).

The density of intermediate-browse tolerant-high shade tolerant trees increased in gap areas significantly more than all other categories (mean=7.04, SE=1.6), not including high browse tolerance, high shade tolerance trees, which saw the next highest increase in the gaps (mean=4.69, SE=2.9) (Table 4).

Patterns in Richness

Although richness either increased or stayed constant in the gap areas across all tree species groups, none of these increases were significantly different from one another (Figure 5).

Patterns in Relative Abundance

In contrast to density, relative abundance significantly differed among browse tolerance levels but not shade tolerance levels, and similarly, there was a significant interaction between browse and shade tolerance (Table 5)

For the relative abundance, the high browse tolerant-high shade tolerant group was significantly less than both the low browse tolerant-low shade tolerant and the intermediate browse tolerant-high shade tolerant groups (intermediate-high:high-high p- value=0.00004; low-low:high-high p-value=0.0127; Figure 3).

Patterns in Sugar Maple Browse

The mean proportion of browsed sugar maples in the gaps was 0.58 with a standard deviation of 0.19 and the mean in non-gap areas was 0.44 with a standard deviation of 0.12. The proportion of sugar maples browsed was significantly higher in canopy gaps than in the surrounding forest area ($t = -9.9096$, $df = 33$, p-value = 1.016e-11; Figure 6).

Discussion

Hypothesis 1: Relative abundance of high-browse tolerant trees without respect to location

The hypothesis that higher browse tolerant species are significantly more common than lower browse tolerant species is supported by the results. The intermediate and high browse tolerant groups had the highest density both in gaps and in non-gaps (Figure 4). Additionally, the highest two tree species groups in gaps and closed canopies were the intermediate browse tolerant-high shade tolerant and high browse tolerant-high shade tolerant groups (Figure 2). This, along with the lack of difference between shade tolerance levels suggest that higher browse tolerance is being selected for regardless of the presence of a canopy gap. Increased deer populations in the area are likely the cause of this shift towards browse tolerance.

Hypothesis 2: Browse prevalence in gaps and Hypothesis 3: Abundance of high-browse tolerant trees with respect to location

The data supports the hypothesis that sugar maple seedlings in gaps are browsed more than seedlings in surrounding forest area (Figure 6). This suggests an increased selective pressure imposed upon seedlings in canopy gaps for browse tolerance. As gaps are considered an important determinant of forest composition and are important for the regeneration of species that can’t regenerate under closed canopy (Schnitzer et al. 2008), over browsing could have serious implications for the survival of various tree species. The densities of intermediate and high browse tolerant species increased the most in gaps. These species may have an advantage in gap areas because of the higher levels of browse. Further study about the relationship between canopy gaps and browsing levels is necessary to provide a more complete picture of the selective pressures acting on trees.

Hypothesis 4: Absolute abundance of shade-tolerant trees with respect to location

The data does not support the hypothesis that shade tolerant species depend upon canopy gaps for their survival, but it does indicate that they take advantage of the resources that gaps provide (Figure 3). The high shade tolerant tree density increased more than any of the other groups but the low shade tolerant pioneers should have seen a significant increase in the gaps (Schnitzer and Carson 2001). However, Nuttle et al. (2013) documented a similar instance where canopy gaps alone failed to increase tree diversity in the presence of deer over browsing. Over browsing by deer may have substantially skewed the relationship between shade tolerance and canopy gaps in this study. An interesting component to study would be if tree species depend on canopy gaps for their survival when deer browsing levels are at a historical level, prior to the relatively recent increase in deer numbers.

Conclusions

Canopy gaps are considered integral to the survival and regeneration of various pioneer tree species (Schnitzer 2001). Over browsing appears to be reducing the positive regenerative effects that canopy gaps have on forest communities (Collins and Carson 2002). The impact that over browsing has on the regeneration of tree species both in canopy gaps and in the closed canopy needs to be understood or some species may be pushed out of forest communities all together. Already, over browsed areas are selecting for high browse tolerance and high shade tolerance even in canopy gaps. If left unchecked, deer over browsing will continue to drastically alter forest composition.

A way build upon this study would be a long term follow up involving experimental manipulation in the form of creating canopy gaps and fencing off areas to control deer browsing. This design would provide experimental information about how browsing and canopy gaps affect the composition of the forest rather than gleaning information observationally. An example of such an experiment is Nuttle et al. (2013) where gaps were created, deer exclosures were used and prescribed fires were utilized. The experimental factors limit the confounding variables and allow for stronger assertions to be made based on the data. This study supports that over browsing impacts the regeneration of trees both in gaps and closed canopy areas and more studies need to be conducted to further analyze how forest composition is being altered by browse.

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Tables

Browse Tolerance	Shade Tolerance	Tree Species	
High	High	Sugar Maple Eastern Hemlock	*Acer saccharum* *Tsuga canadensis*
High	Intermediate	White Spruce	*Picea glauca*
High	Low	None	
Intermediate	High	Basswood Balsam Fir Hop Hornbeam	*Tilia americana* *Abies balsamea* *Ostrya virginiana*
Intermediate	Intermediate	Eastern White Cedar Red Maple	*Thuja occidentalis* *Acer rubrum*
Intermediate	Low	Paper Birch	*Betula papyrifera*
Low	High	None	
Low	Intermediate	Yellow Birch Eastern White Pine	*Betula alleghaniensis* *Pinus strobus*
Low	Low	Quaking Aspen Bigtooth Aspen White ash Black Cherry	*Populus tremuloides* *Populus grandidentata* *Fraxinus americana* *Prunus serotina*

Table 1: Tree species categories for browse and shade tolerance. Categories labelled with browse and shade tolerance levels respectively.

		Chi-squared	DF	p-value
Relative Abundance	Shade Tolerance	17.817	28	0.9307
	Browse Tolerance	18.699	45	0.9998
Species Richness	Shade Tolerance	0.67707	3	0.8786
	Browse Tolerance	2.0973	2	0.3504
Density	Shade Tolerance	9.0057	10	0.5316
	Browse Tolerance	27.169	20	0.1306

Table 2: Results from Fligner-Killen test for homogeneity of variances. All tested variances were homogenous allowing for ANOVA to be used.

	Sum Sq	Df	F value	Pr(>F)
Browse Tolerance	118.8	2	1.6836	0.1880300
Shade Tolerance	634.3	2	8.9905	0.0001753 ***

Browse Tolerance : Shade Tolerance	608.7	4	4.3137	0.0022117 **

Table 3: ANOVA results for density comparison of different shade tolerance and browse tolerance levels.

Browse-Shade:Browse-Shade	Difference	Lower	Upper	P-values
intermediate-high:low-high	-7.038	-12.198	-1.878	0.000941
intermediate-high:high-intermediate	-7.076	-12.236	-1.917	0.000856
intermediate-high:intermediate-intermediate	-6.692	-11.851	-1.532	0.00215
intermediate-high:low-intermediate	-6.653	-11.813	-1.494	0.00235
intermediate-high:high-low	-7.038	-12.198	-1.878	0.000941
intermediate-high:intermediate-low	-6.961	-12.121	-1.801	0.00113
intermediate-high:low-low	-5.192	-10.351	-0.0327	0.0472

Table 4: Significant p-values for density two-way ANOVA Tukey HSD multiple comparison.

	Sum Sq	Df	F value	Pr(>F)
Browse Tolerance	0.2440	2	3.7318	0.0254439 *
Shade Tolerance	0.0230	2	0.3522	0.7035131
Browse Tolerance : Shade Tolerance	0.6367	2	4.8692	0.0008754 ***

Table 5: ANOVA results for relative abundance difference between gap and non-gaps. Significant differences were observed across browse tolerance levels and in the browse tolerance-shade tolerance interactions.

Figures

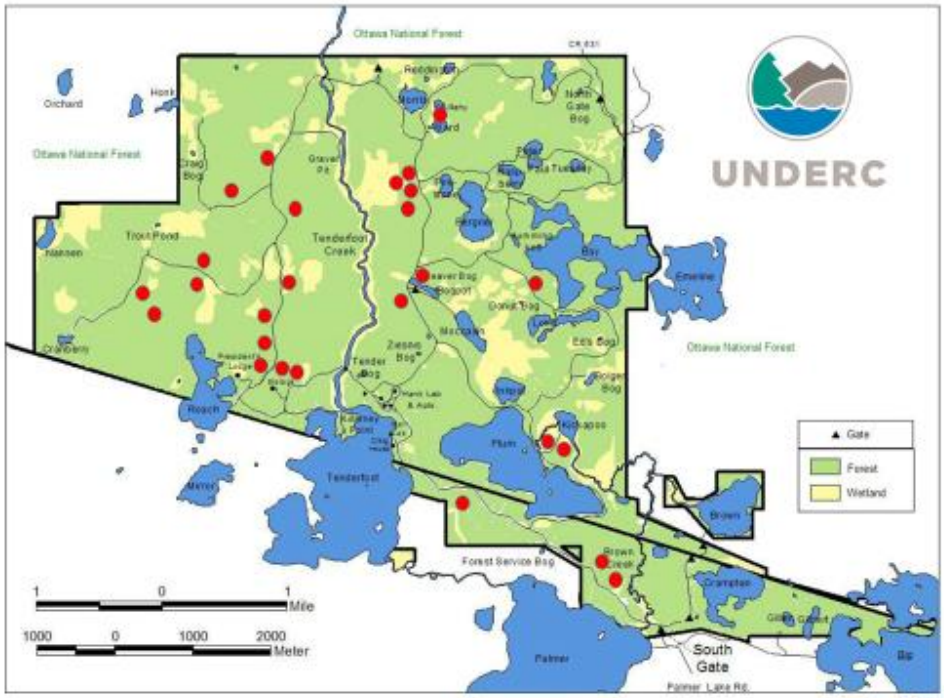

Figure 1: Map of study area with sample site locations shown with red dots.

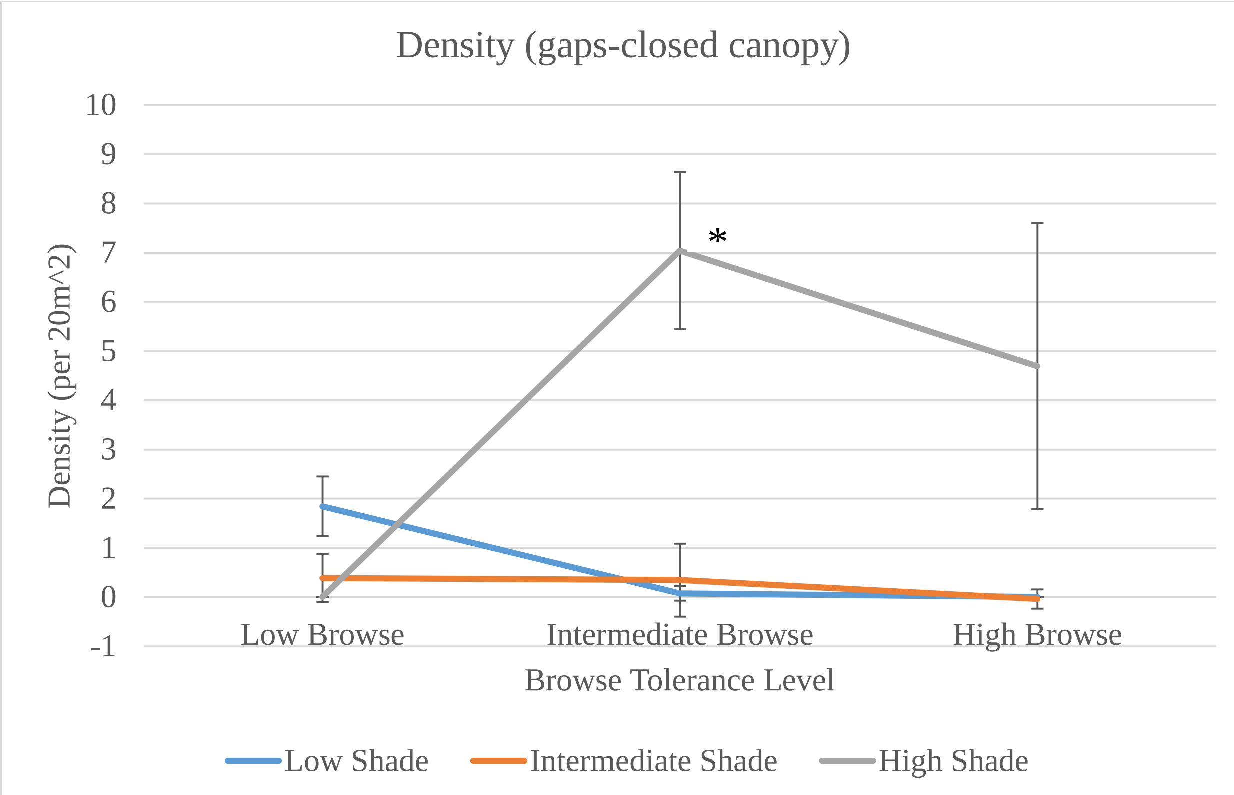

Figure 2: Density increase in canopy gaps vs. closed canopy for shade and browse tolerance levels. * marks significant difference from other groups, excluding high browse tolerance-high shade tolerance group.

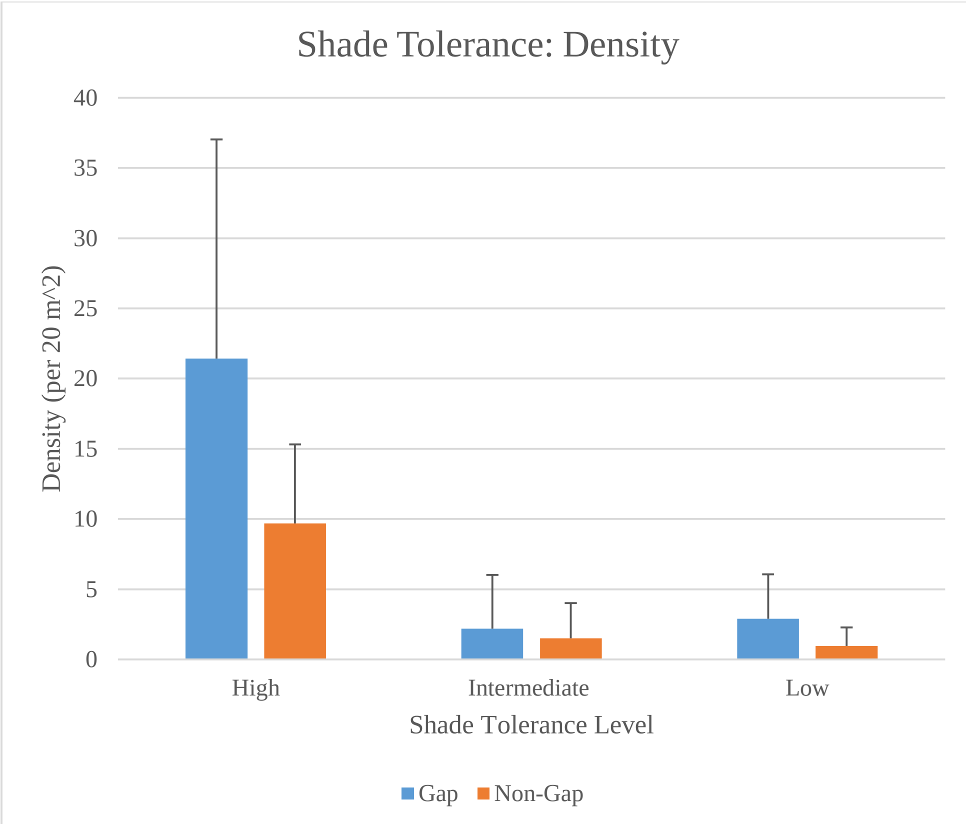

Figure 3: Density of species by shade tolerance level in gaps vs. in non-gaps.

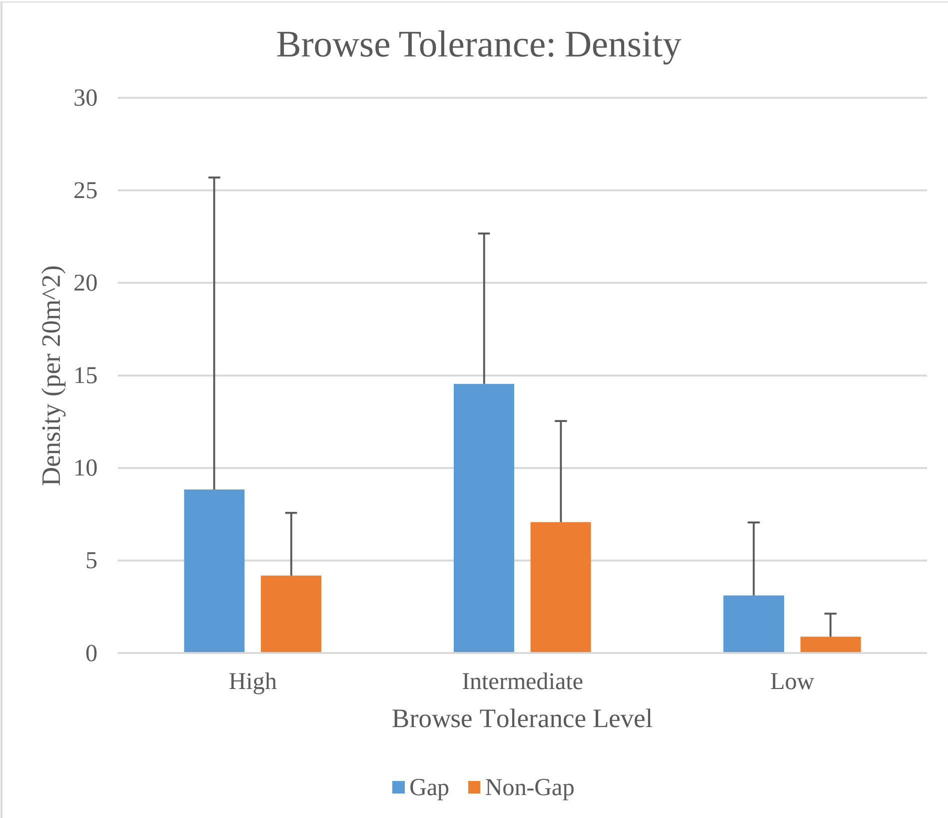

Figure 4: Density of tree species by browse tolerance level in gaps vs. in non-gaps.

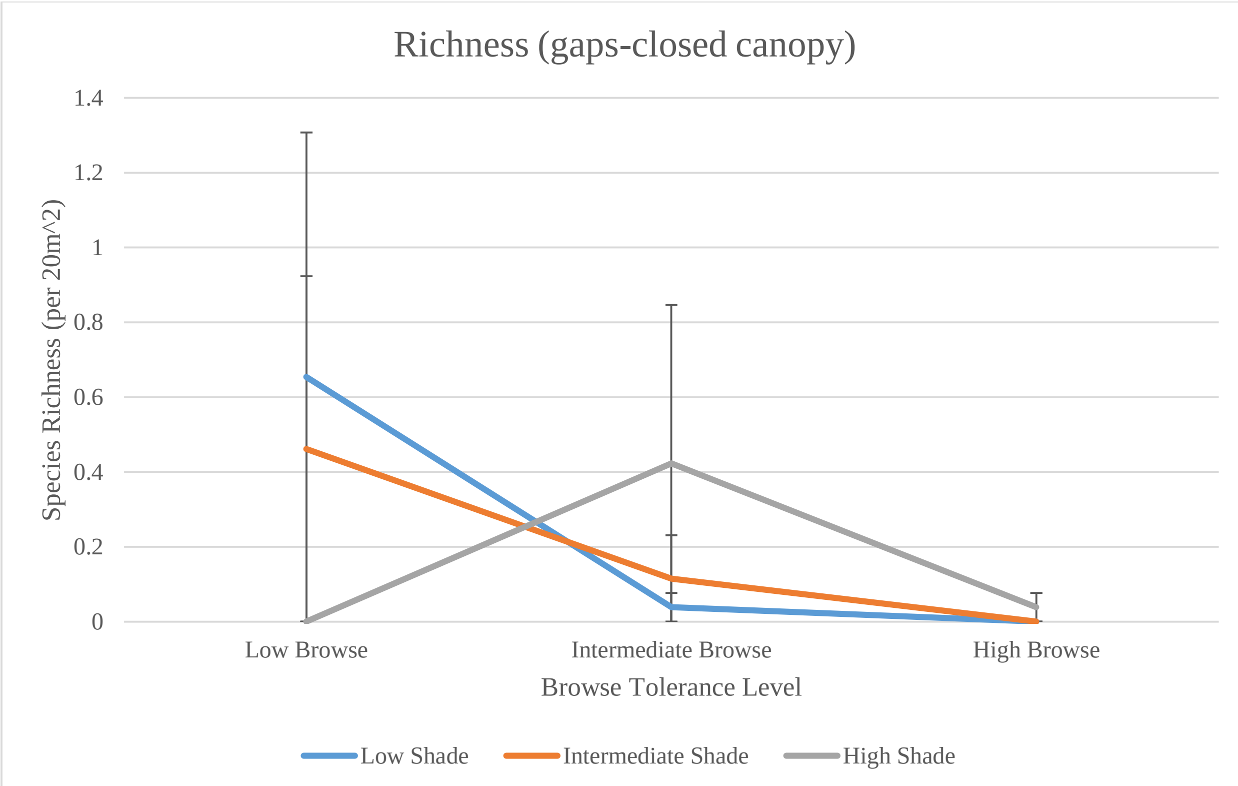

Figure 5: Richness increase in canopy gaps vs. closed canopy for shade and browse tolerance levels. No significant differences across groups.

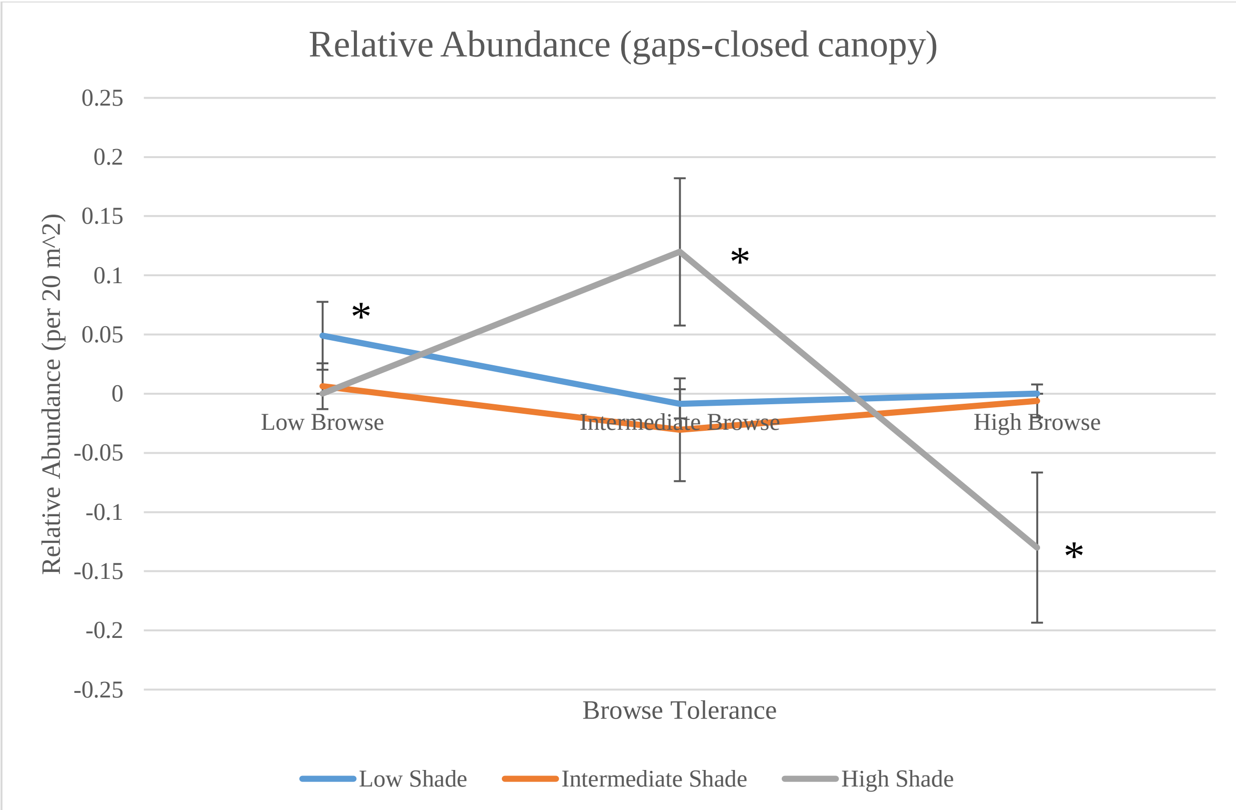

Figure 6: Relative abundance increase in canopy gaps vs. closed canopy for shade and browse tolerance levels. * marks significant difference of low-low:high-high (Tukey test, p =0.0127), intermediate-high:high-high (Tukey test, p =0.0000433).

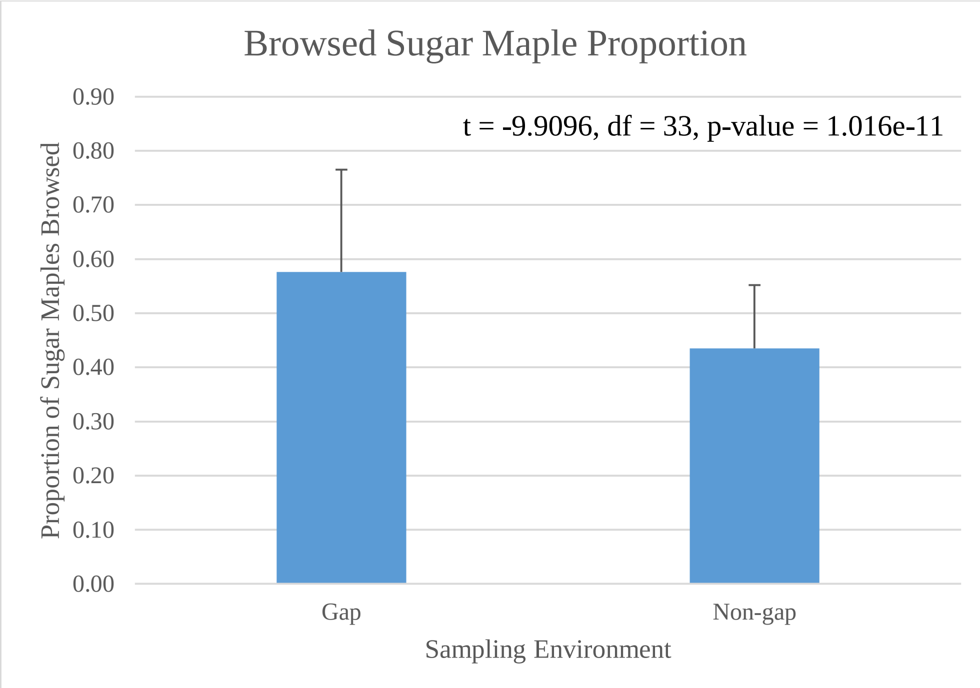

Figure 7: Comparison of the proportion of sugar maple seedlings browsed in canopy gaps and in the surrounding forest area.

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